

A taphonomic and zooarchaeological study of Pleistocene fossil assemblages from the western Nefud Desert, Saudi Arabia

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A taphonomic and zooarchaeological study of Pleistocene fossil assemblages from the western Nefud Desert, Saudi Arabia

Mathew Stewart

A thesis in fulfillment of the requirements for the degree of

Doctor of Philosophy



School of Biological, Earth and Environmental Sciences

PANGEA Research Centre

University of New South Wales

November 2018

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Despite its geographical positioning at the crossroads of Africa and Eurasia, the Arabian Peninsula has been largely absent from models regarding hominin out of Africa dispersals and evolution. However, a recent upturn in archaeological and palaeoenvironmental research is providing a platform with which to consider Arabia into these debates. This thesis aims to address one of the remaining gaps in the Arabian record - that of palaeontology - by investigating Pleistocene fossil deposits from the western Nefud Desert, Saudi Arabia. In Chapter Two, I conduct an extensive review of the Pleistocene mammal fossil record from Arabia and the surrounding regions. This review highlights the composite nature of the Arabian fossil record, significant climate-induced faunal turnover in Africa, and relatively stable conditions in Southwest and South Asia. In Chapter Three, my colleagues and I conduct stable isotope analysis of fossil fauna associated with newly discovered stone tools and probable butchery marks. Results demonstrate that conditions were comparable to modern-day East African savannas, suggesting hominin dispersals into the region required no major novel adaptations. In Chapters Four, Five, and Six, I conduct detailed taxonomic and taphonomic analyses to provide insights into past environmental conditions and site formation processes. Results indicate

that bones accumulated in conditions more humid and vegetated than the present day, while more recent processes such as wind and salt weathering have drastically altered fossil appearance and composition. In *Chapter Five*, I report hominin and non-hominin mammal tracks and trackways. The age of the tracks implies *Homo sapiens* was the probably trackmaker, while analysis of the track assemblage suggests that *H. sapiens* and large mammals were occupying and utilizing similar spaces and resources at the same times. The age of the tracks also suggests the earliest *H. sapiens* dispersals out of Africa were not restricted to the Levant but extended into the Arabian interior. Taken together, these studies provide unique and detailed insights into the interplay between hominins, animals, and the environment within the Arabian interior and have shed considerable light on some of palaeoanthropology's outstanding questions.

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Stewie

ABSTRACT

Despite its geographical positioning at the crossroads of Africa and Eurasia, the Arabian Peninsula has been largely absent from models regarding hominin out of Africa dispersals and evolution. However, a recent upturn in archaeological and palaeoenvironmental research is providing a platform with which to consider Arabia into these debates. This thesis aims to address one of the remaining gaps in the Arabian record – that of palaeontology – by investigating Pleistocene fossil deposits from the western Nefud Desert, Saudi Arabia. In Chapter Two, I conduct an extensive review of the Pleistocene mammal fossil record from Arabia and the surrounding regions. This review highlights the composite nature of the Arabian fossil record, significant climate-induced faunal turnover in Africa, and relatively stable conditions in Southwest and South Asia. In Chapter Three, my colleagues and I conduct stable isotope analysis of fossil fauna associated with newly discovered stone tools and probable butchery marks. Results demonstrate that conditions were comparable to modern-day East African savannas, suggesting hominin dispersals into the region required no major novel adaptations. In *Chapters Four*, Five, and Six, I conduct detailed taxonomic and taphonomic analyses to provide insights into past environmental conditions and site formation processes. Results indicate that bones accumulated in conditions more humid and vegetated than the present day, while more recent processes such as wind and salt weathering have drastically altered fossil appearance and composition. In Chapter Five, I report hominin and non-hominin mammal tracks and trackways. The age of the tracks implies *Homo sapiens* was the probably trackmaker, while analysis of the track assemblage suggests that *H. sapiens* and large mammals were occupying and utilizing similar spaces and resources at the same times. The age of the tracks also suggests the earliest H. sapiens dispersals out of Africa were not restricted to the Levant but extended into the Arabian interior. Taken together, these studies provide unique and detailed insights into the

interplay between hominins, animals, and the environment within the Arabian interior and have shed considerable light on some of palaeoanthropology's outstanding questions.

CONTENTS

LIST OF	FIGURES I
LIST OF	TABLESVII
LIST OF	APPENDICES XIII
СНАРІ	TER
1.	General introduction1
2.	Middle and late Pleistocene mammal fossils of Arabia and surrounding regions: Implications for biogeography and hominin dispersals
3.	Fossil herbivore stable isotopes reveal middle Pleistocene hominin palaeoenvironment in 'Green Arabia' 109
4.	Taphonomic and zooarchaeological investigations at the middle Pleistocene site of Ti's al Ghadah, western Nefud Desert, Saudi Arabia
5.	Human footprints provide snapshot of penultimate interglacial ecology in the Arabian interior
6.	Fossils in the desert: A taxonomic and taphonomic study of fossil deposits from the western Nefud Desert, Saudi Arabia
7.	Summary and general conclusions

LIST OF FIGURES

CHAPTER ONE

CHAPTER TWO

Figure 1

Map of	f major	sites	discussed	in th	e text	;	40)
--------	---------	-------	-----------	-------	--------	---	----	---

Figure 2

Figure 3

Temporal	distribution	of major	non-bovid	ungulates,	Proboscidea	and
carnivores	from region	s discusse	ed in the te	xt		73

CHAPTER THREE

Long bone notch morphology compared to those generated by carnivores
and hominins under experimental settings137

Figure 5

 $\delta^{13}C$ and $\delta^{18}O$ measurements from tooth-enamel of fossil fauna 140

Figure 6

Figure 7

Sequential	$\delta^{13}C$	and	$\delta^{18}O$	measur	ements	for	fossil	Oryx	sp.	and	one
modern Org	yx leu	coryx	;	• • • • • • • • • • • • • • •	•••••					•••••	145

Figure 8

Sequential	$\delta^{13}C$	and	$\delta^{18}O$	measurements	for	fossil	Palae oloxodon
sp							146

Figure S1

An	example	Fourier-T	ransform	Infrared	Spectroscopy	(FTIR)	plot of
mo	dern and f	fossil taxa					165

Figure S2

Boxplots of infrared indexes (API,	BPI, BAI,	PCI and	ISRF) for	modern
and fossil Arabian fauna				166

CHAPTER FOUR

Figure 1

Oblique 3-D map of the Ti's al Ghadah basin highlighting	the location of
the various fossil deposits	

Stratigraphic	log	of	Ti's	al	Ghadah	showing	the	sedimentology	of
exposed sands	and	ma	arls					1	95

Figure 3

Oryx mandibular fossils	
-------------------------	--

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Frequency of tooth-marked medium-sized animal long bones, midshaft fragments, and epiphyses compared to experimental scenarios modelling carnivore primary and secondary access to carcasses243

Figure 12

Example of polish and pitting resulting from abrasion by fine wind-b	olow
sand	249

Figure S1

Summary	diagram	of	the	Ti's	al	Ghadah	Iron	Lake	(TIL)	diatom
assemblag	e		•••••		••••		•••••			283

Figure S2

Summary	diagram	of	the	Ti's	al	Ghadah	Unit	6	diatom
assemblage	9							•••••	

Figure S3

Fossil Alcelaphinae tooth dimensions compared to comparative morphometric data from various extant species of Alcelaphinae.......286

Figure S4

Figure S5

Distribution of frequencies (%NISP)	for specimen length for the TLS and	nd
TSR assemblages		88

CHAPTER FIVE

Figure 1

Figure 3

Representative	photo-micrographs	in	cross-polarised	light	of	the
Alathar palaeola	ake sediments					315

Figure 4

Figure 5

Figure 6

Figure 7

Protocol used in the collection of hominin track morphometric dat	a and	
selected photographs of hominin tracks	336	;

Figure 8

Figure 9

Figure 10

Stable carbon (δ^{13} C) and oxygen (δ^{18} O) isotope values for herbivore tee	eth
analysed in the present study3	342

Figure S1

Figure S2

Abanico plots displaying t	ne spread of D _e	e values observed	in samples
PD60, PD61, and PD62			

Figure S3

Sequential stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}C$	0) isotope measurements
from fossil Elephantidae	

CHAPTER SIX

Figure 1

Map	of	the	western	Nefud	Desert	displaying	the	location	of	sites
discu	sse	d in [.]	the text							377

Figure 2

Satellite	image	and	full	sedimentary	sequences	of	the	fossil	bearing
lakes at 1	Khall A	may	shan	-4 (KAM-4)					380

Figure 3

Figure 4

Principal component analysis (PCA) for five metric va	ariable of fossil
intermediate phalanx (KAM16/272) and comparative da	ata from extant
and extinct Equus spp	

Figure 5

Selected	fossils	from	Khall	Amayshan-4,	16.3,	WNEF16_1,	and
WNEF16	_25						. 394

Figure 6

Selected Hippopotamus	fossils	395
-----------------------	---------	-----

Selected examples of bone surface modifications; car	mivore gnaw marks,
weathering, root etching, wind abrasion, bleaching,	manganese staining
and crushing	

LIST OF TABLES

CHAPTER THREE

Table 1

Summary of the chronological data available for Ti's al Ghadah......126

Table 2

Annual	mean	temperat	ture (A	MT)	and	annual	average	precipitation
(MAP) fo	or mod	ern sites	used in	h this	study	y		131

Table S1

Table S2

Table S3

Table S4

Table S5

Table S6

Sequential	$\delta^{13}C$	and	$\delta^{18}O$	measuren	nents	from	modern	Oryx	leucoryx

Table S7

Results	of	the	mixed	ANOVA	for	$\delta^{18}O$	by	group	(obligate	and
non-oblig	gate	e drin	k) by si	te						.175

Table S8

Results of the post-Hoc Tukey pairwise comparison for δ^{1}	¹⁸ O by group
(obligate and non-obligate drinker) by site	176

Table S9

Infrared indexes (API, BPI, BAI, PCI, WAMPI) for sample groups subjected to Fourier-Transform Infrared Spectroscopy (FTIR)177

Table S10

CHAPTER FOUR

Table 1

Complete taxonomic list of the Ti's al Ghadah fossil assemblages.....217

Table 2

Species representation according	to NISP	and MNI	for the	Unit 5	and
Elephant Quarry assemblages					.219

Table 3

Results of the Unit 5 taphonomic analysis by animal size class 221

Table 4

Table 5

Chi-squared test comparisons of shaft ratio for the Unit 5, TSR, TLS,
and experimental scenarios modelling carnivore primary and secondary
access to carcasses

Table 6

Table 7

Table 8

Table 9

Results of the TSR and TLS taphonomic analysis251

Table 10

TSR and TLS skeletal part representation......252

Table 11

Basic	typological	composition	of	the	Ti's	al	Ghadah	lithic
assemb	olages			•••••	•••••			255

Table 12

Raw material composition of the Ti's al Ghadah lithic assemblages .256

Table 13

Comparison of basic flake dimensions for each lithic assemblage $\dots 258$

Table S1

Unit 5 medium-sized ungulate skeletal part representation......289

Table S2

Unit 5 small- and medium-sized bovid limb bone portion abundance
(MNE) and corresponding goat and wildebeest bone mineral density
values

Table S3

Unit 5 small- and medium-sized bovid skeletal part representation	n and
corresponding standard food utility index	292

Table S4

Unit	5	to oth-marked,	probable	cut-marked,	and	percussion-marked
bones	s b:	roken down by a	animal siz	e class		

Table S5

Unit	5	tooth-marked,	probable	cut-marked,	and	percussion-marked
bones	s b	roken down by t	rench			

CHAPTER FIVE

Table 1

Summary optically stimulated luminescence (OSL) dating results and ages
Table 2
Results of the taphonomic analysis
Table 3
Complete skeletal inventory (NISP) broken down by animal size class
Table 4
List of fossil and ichnofossil taxa
Table 5
Hominin stature, mass, and speed estimates

Table 6

Alathar homi	nin footprint :	morphometric	data	7
--------------	-----------------	--------------	------	---

Table 7

Table S1

Table S2

Table S3

Optically stimulated luminescence (OSL) sample depths,	, water content
and dose rat	

Table S4

$\delta^{13}C$ and $\delta^{18}O$	measurements of fossil faunal	
-----------------------------------	-------------------------------	--

Table S5

Sequential $\delta^{13}C$ and $\delta^{18}O$ measurements of fossil Elephantidae.......367

Table S6

CHAPTER SIX

Table 1

Fossil	Hippopotamus	amphibius	third	metacarpal	(KAM-1/F34)
morpho	metric data				

Table 2

Fossil <i>Hippopotamus amphibius</i> astragali (16.3/51, 210, 437) morphometric data
Table 3
Fossil <i>Hippopotamus amphibius</i> metapodial (16.3/33, 84, 111, 385) morphometric data
Table 4
Fossil <i>Pelorovis</i> sp. morphometric data
Table 5
Fossil <i>Oryx</i> sp. horn core morphometric data
Table 6
Taxonomic list
Table 7
Skeletal part representation (NISP)
Table 8
Results of the taphonomic analysis
Table 9
Distribution of frequencies (%NISP) for specimen length
Table 10
KAM-4 NW lake medium-sized bovid minimum number of elements
(MNE) for selected limb bones
Table 11
Chi-squared test results of long bone shaft completeness compared to
experimental scenarios modelling carnivore primary and secondary

Table S1

KAM-4	NW	lake	equi	d	intermediate	phalanx	(KAM	16/27	72)	and
compara	ative	data	from	<u>ht</u>	tp://www.vera-	eisenman	<u>n.com/</u>	and	Alb	erdi
and Pal	ombo	(2013)					•••••		.435

Table S2

Lis	st of a	accessio	on numbers for	specimen	s used as	com	parative	material
in	this	study	(Smithsonian	National	Museum	of	National	History
[N	MNH	[])				•••••		

LIST OF APPENDICES

CHAPTER THREE

Appendix A	
Isotope analysis results	165
Appendix B	
Dated Arabian palaeohumidity proxy data	178
CHAPTER FOUR	

Appendix A	
Diatom analysis results	
Appendix B	
Taxonomic and taphonomic analysis results	

CHAPTER FIVE

Appendix B

Results of stable carbon (δ^{13} C) and	d oxygen (δ ¹⁸ O)	analysis	
Appendix C			

CHAPTER SIX

Appendix A

CHAPTER SEVEN

Appendix A

A list of publications that developed during my doctoral studies......448

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CHAPTER ONE

General introduction

Mathew Stewart

Hominin prehistory and dispersals

Orbitally-forced increases in environmental variability and open grassland habitats during the Pliocene (c. 5.3–2.9 million-years-ago, or Ma) and Pleistocene (c. 2.8–0.01 Ma) resulted in the significant restructuring of African large mammal communities (Vrba, 1985, 1992, 1993; Potts, 1998; Bobe and Behrensmeyer, 2004; deMenocal, 2004). It was around the transition between these two epochs that some of the most significant developments in hominin prehistory occurred – the arrival of our genus (Homo) and the origins of stone tool technologies. Not long after this, Homo extended its range into Eurasia (Gabunia et al., 2000; Zhu et al., 2008, 2015; Zaim et al., 2011) and recently discovered lithic artefacts from Central China, dated to c. 2.1 Ma, provide the earliest documented evidence for the out of Africa exodus of our genus (Zhu et al., 2018). This initial dispersal (or "Out of Africa 1") was succeeded by subsequent inter- and intracontinental movements throughout the Pleistocene, leading up to the out of Africa dispersal of our own species (or "Out of Africa 2") by c. 130 ka (Grün et al., 2005), and perhaps as early as c. 180 ka (Hershkovitz et al., 2018). Most researchers maintain that most intercontinental hominin and faunal movements passed through the Sinai Peninsula and southern Levant, the only secure land-bridge between African and Eurasia since the Miocene (Fernandes et al., 2006). Perhaps unsurprisingly, this region has received considerable scientific attention over the past century, resulting in what many would consider some of palaeoanthropology's most significant findings (e.g. the Skhul and Qafzeh hominins [Grün et al., 2005]). Despite this, there is little consensus as to the timing and nature of hominin evolution and dispersal between these continents.

Introduction

Debates regarding this tend to focus on intrinsic and extrinsic factors as the driving mechanism behind early Homo (H. habilis + H. rudolfensis + H. erectus) movements (Belmaker, 2017). The former maintain that early Homo was well-adapted to, but largely reliant on, 'savanna' environments: defined here as "mixed tree-grass systems characterized by a discontinuous tree canopy in a continuous grass layer" (Ratnam et al., 2011: p. 653). In this view, dispersals beyond Africa were dependent on the spread of the African savannas ("common African home hypothesis") and associated fauna ("migratory wave hypothesis") into Eurasia (Tchernov, 1992; Dennell, 2004; Martinez-Navarro, 2010; Leroy et al., 2011). Dennell and Roebroeks (2005) proposed that a large 'Savannahstan' extended across North Africa, Arabia, and South Asia at times during the Pleistocene. Such conditions would have allowed savanna adapted fauna and hominins to move between the continents relatively unhindered, and evidence for such dispersals is present in the fossil record (e.g. Tchernov, 1986; Martínez-Navarro, 1992, 2010; Dennell, 2004; Rook et al., 2004). Some have argued that early Homo were obligate scavengers in East Africa that dispersed out of Africa alongside large carnivores (Turner, 1992; Arribas and Palmqvist, 1998), while others maintain that they were efficient hunters that followed medium- and large-sized herbivores (Rolland, 2010).

Alternatively, it has been suggested that early *Homo* movements were not tied to that of other animals (Bar-Yosef and Belfer-Cohen, 2001; Belmaker, 2010). Some researchers have argued that the Plio-Pleistocene Afro-Eurasian faunal exchanges were highly complex with few species moving in concert and with no evidence for 'migratory waves' (Agustí and Lordkipanidze, 2011; O'Regan et al., 2011; Palombo, 2013). Furthermore, fauna and other palaeoenvironmental data from Eurasian sites central to this ongoing debate (e.g. Dmanisi, 'Ubeidiya) have been argued to signal relatively humid

Introduction

Mediterranean woodland conditions, suggesting a uniquely Eurasian setting immediately beyond Africa (e.g. Gabunia et al., 2000; Belmaker, 2010; Messager et al., 2011). In this view, early *Homo* exhibited a level of dietary, developmental, technological, and/or behavioural flexibility that enabled it to exploit a broad spectrum of habitats ranging from open grasslands to dense forests (Potts, 1998, 2012; Carbonell et al., 2010; Agustí and Lordkipanidze, 2011; Palombo, 2013; Antón et al., 2014). Indeed, hominins have been found in a variety of palaeoenvironmental settings, our understandings of which have fluctuated, and at times changed, due to a developing appreciation of the complexity of obtaining accurate and precise habitat information from palaeoenvironmental data spanning different temporal and spatial scales (Reed, 1997; Potts, 2013; Roberts and Stewart, 2018).

Taphonomic studies are powerful tools for elucidating the ecological interactions between hominins, animals, and the environment (Pante et al., 2012) and have been central in discussions surrounding early Homo evolution. Hominins and carnivores systematically process carcasses in ways that reflect species-specific feeding behaviours, order of access, and inter- and intra-taxon interactions (e.g. competition). The early recognition of this prompted a series of experimental and naturalistic studies that set out to identify how different bone accumulators and modifiers might be differentiated from the fossil record (e.g. Blumenschine, 1986, 1988; Stiner, 1990; Marean and Spencer, 1991; Marean et al., 1992; Selvaggio, 1994). These studies demonstrated that the kinds of prey animals and their ages (e.g. Stiner, 1990; Bunn and Pickering, 2010), skeletal part representation and fragmentation (e.g. Blumenschine, 1986, 1988; Marean and Spencer, 1991; Marean et al., 1992), and the types of bone surface modifications, their locations, and frequencies (e.g. Blumenschine, 1986, 1988; Capaldo, 1997; Domínguez-Rodrigo, 1999) provide reliable insights into the agent(s)

responsible for the accumulation of bone assemblages. For example, it has been demonstrated that hyenas differentially damage bones depending on whether they have primary or secondary access to carcasses (Blumenschine, 1988; Capaldo, 1997). More specifically, hyenas that encounter defleshed and demarrowed long bones tend to ignore midshaft fragments as these obtain little nutritional value, which is reflected in the low number of tooth-marked midshafts when compared to hyenas fed fleshed bones. These frameworks have been variously applied to investigate the role of early *Homo* in the carnivore guild: was early *Homo* an effective hunter or was it restricted to scavenging from the kills of other carnivores, and what does this mean for its evolution and dispersal capabilities? (I refer readers to the historic and ongoing hunting versus scavenging debate surrounding early *Homo* behaviour at the early Pleistocene FLK *Zinjanthropus* site, Olduvai Gorge [e.g. Bunn, 1981; Binford, 1986, 1988; Domínguez-Rodrigo and Barba, 2006; Pante et al., 2012, 2015; Domínguez-Rodrigo et al., 2014).

The nature and timing of the dispersal of *Homo sapiens* beyond Africa is equally contentious. Models again fall into or across two broad categories emphasizing either an early (c. 130–75 thousand-years-ago, or ka) or late (c. 60–50 ka) dispersal out of Africa. According to late dispersal models, the arrival of *Homo sapiens* in the Levant c. 130–80 ka is viewed as a short-lived range expansion and precursor to the eventual 'successful' out of Africa dispersal c. 60 ka that gave rise to all non-African *Homo sapiens* (Shea, 2008; Mellars et al., 2013). Similarly, faunal evidence has been used to argue that this initial *H. sapiens* dispersal was largely contingent on the out of Africa spread of the savanna grasslands and grassland adapted taxa (Tchernov, 1992). But this idea has been disputed given the overall Eurasian nature of the fauna at non-African sites key to this debate (Stewart et al., 2017). Conversely, the Levantine early *H. sapiens* fossils are thought to mark the
onset of a much broader expansion into Eurasia that started around c. 130-90 ka (Groucutt et al., 2015; Bae et al., 2017; Rabett, 2018). This has gained support from recent fossil (Liu et al., 2015; Westaway et al., 2017; Groucutt et al., 2018) and archaeological (Clarkson et al., 2017) discoveries in Asia and Australia that appear inconsistent with an exclusively late dispersal, and noteworthy is this recent fossil findings from Misliya Cave in Israel, dated to c. 177 ka, that points to an even earlier out of Africa dispersal event (Hershkovitz et al., 2018; but see Sharp and Paces, 2018). Furthermore, recent interpretations of genetic data can also be considered consistent with an earlier dispersal (Groucutt et al., 2015; Pagani et al., 2016), although overall genetic data remains equivocal on the question of timing of Out of Africa 2 (Rabett, 2018; Scerri et al., 2018).

The route(s) through which *H. sapiens* left Africa also remains an open-ended and hotly debated area of inquiry (Groucutt et al., 2015; Bae et al., 2017). Coastal regions have featured prominently in models of H. sapiens dispersals out of Africa (e.g. Stringer, 2000; Armitage et al., 2011; Mellars et al., 2013; Erlandson and Braje, 2015). Notably, the "southern dispersal route hypothesis" proposes that H. sapiens rapidly skirted along the coasts of Arabian Peninsula and the Indian Ocean rim on their way to Sahul (Mellars et al., 2013). Others have persuasively criticised coastal dispersal models in favour of inland routes through the Sinai Peninsula, drawing on archaeological evidence and disputing the idea that coastal regions represent stable oases with bountiful resources (Westley and Dix, 2006; Boivin et al., 2013; Groucutt et al., 2015; Rabett, 2018). The long-held view that the diffusion and eventual geographic dominance of all non-African H. sapiens was the result of a single major dispersal event is also being challenged. Evidence for multiple out of Africa dispersals, back migrations, and genetic admixture events between *H. sapiens* and contemporary hominins in Asia is

revealing a far more complex picture than originally assumed (see Bae et al., 2017 for recent review). This new data is challenging many of our current migration models and preconceptions about the evolution and movements of our species within and outside of Africa (Bae et al., 2017; Henn et al., 2018; Scerri et al., 2018;).

In spite of its geographical position at the crossroads of Africa and Eurasia, the Arabian Peninsula has, until relatively recently, been largely absent from discussions regarding hominin and animal movements between the continents. However, an upturn in archaeological, palaeoenvironmental, and palaeontological research in the region is providing a unique opportunity to factor Arabia into these debates. The studies presented in this thesis are an addition to this effort.

Study area

The Arabian Peninsula (often simplified as 'Arabia'), situated at the nexus of Africa and Eurasia, covers an area of more than 3 million km². This vast region is characterised by a mosaic of habitats: semi-tropical and montane regions run along the southern and western coasts, the southwestern highlands of 'Asir and Yemen approach forest-like conditions, while vast swaths of the interior are dominated by hyper-arid sand seas (or ergs) (Edgell, 2006; Vincent, 2008). The sites presented in this thesis are located in the Nefud Desert (or An Nafud), situated in the northwest of the peninsula (Fig. 1).

The Nefud Desert is the second largest sand sea in Arabia, occupying an area of around 57,000 km². The dune sands are Quaternary in age and originate from the erosion of extensive outcrops of Palaeozoic sandstones that

lie to the west and northwest of the present-day dune field (Edgell, 2006; Vincent, 2008). Mean annual rainfall across the Nefud Desert is 80-90 mm/year with increasing rainfall moving west to east. The sites reported here lie in the more arid western Nefud Desert which receives as little as 30 mm/year (Edgell, 2006). The dune field is filled with fragmentary geological material that is thought to be the result of extreme diurnal temperature fluctuations (Edgell, 2006). Winter temperature can reach below freezing and snow sometimes falls across northern Arabia, while strong winds between February and June occasionally incite severe sandstorms (Edgell, 2006). The region is dominated by tightly packed transverse and barchanoid dunes that reach heights of up to 200 m (Vincent, 2008). The dune field is considered largely inactive, but smaller active dunes do sit atop the larger stable dunes (Edgell, 2006). Regional vegetation is characterised by sparsely populated semi-arid shrubs (e.g. Calligonum) and grasses (e.g. Stipagrostis), but a variety of grasses and herbs spring up following significant rainfall events (Schulz and Whitney, 1985, 1986), which can produce standing water that persists on playas for months (Breeze et al., 2017).



Figure 1. Map of Arabia highlighting the study area (red rectangle).

Early and recent research in Arabia and its growing importance in palaeoanthropology

Hints of Arabia's wetter past were first documented by 19th and early 20th century explorers who noted ancient lake deposits within the Arabian deserts (Philby, 1933). Lithic artefacts indicating the presence of prehistoric hominins in Arabia were also first reported around this time (Caton-Thompson and Gardner, 1939). Archaeological research in the region remained scarce until the 1970s, which saw the first large-scale surveys of the region and the discovery of a wealth of Palaeolithic material (Groucutt and Petraglia, 2012). These early efforts were complemented by contemporary palaeoenvironmental studies of palaeolake deposits in the Empty Quarter (or Rub' al Khali) and Nefud Desert (McClure and Swain, 1974; McClure, 1976, 1978, 1984; Whitney, 1982, 1983). Radiocarbon dating tied lake formation to the terminal Pleistocene and Holocene, while studies of palaeolake sediments indicated that some of these lakes were large, perennial, and comprised freshwater (McClure and Swain, 1974; McClure 1976, 1984; Whitney, 1982, 1983; Schulz and Whitney, 1986; but see Rosenberg et al., 2011). Freshwater lakes would have provided a vital resource and habitable landscape for hominins and animals alike. Mammalian fossil remains found associated with these palaeolake deposits (e.g. Hippopotamus, Palaeoloxodon, Pelorovis) also indicate much more humid and vegetated conditions than those that characterise these regions today (McClure, 1984; Thomas et al., 1998).

The turn of the millennium saw another upturn in scientific curiosity, and the first truly systematic and interdisciplinary studies (Groucutt and Petraglia, 2012). In addition to the extensive archaeological surveys, developments in palaeoenvironmental studies have been notable, such as the

study of cave speleothem deposits, climate modelling, and remote sensing (e.g. Fleitmann et al., 2003, 2011; Rosenberg et al., 2011, 2013; Breeze et al, 2015, 2016; Jennings et al., 2015; Parton et al., 2015, 2018). To surmise, the palaeoenvironmental data indicate seesaw-like fluctuations between wet (interglacial) and dry (glacial) phases during the middle and late Pleistocene. Such vastly different conditions facilitated an influx of novel fauna and flora and may have driven speciation; the latter has been alluded to by previous researchers based on enigmatic bovid remains recovered from the middle Pleistocene site of Ti's al Ghadah (Thomas et al., 1998; Stimpson et al., 2016). Faunal influxes likely followed palaeohydrological corridors that connected the Arabian interior to northeast Africa and the Near East during humid phases (Breeze et al., 2016). Indeed, the northward extension of the African savannas and associated fauna during interglacials is well-documented in the adjacent Sahara Desert (Drake et al., 2011, 2013 and references therein) and the climatic amelioration of the arid Saharo-Arabian belt would have directly connected Arabia to northern Africa.

Included in these influxes were hominins, with recent archaeological research clearly demonstrating repeated dispersals into the region during the middle and late Pleistocene (e.g. Armitage et al., 2011; Groucutt and Petraglia, 2012; Petraglia et al., 2012), and perhaps even earlier (Bailey et al., 2015; Scerri et al., 2015). Lower Palaeolithic artefacts are documented from across Arabia, but the makers of this technology remain elusive in the absence of fossil evidence (e.g. Petraglia, 2003; Groucutt and Petraglia, 2012; Shipton et al., 2014, 2018). The same remains the case for much of the Arabian Middle Palaeolithic, which are often attributed to *H. sapiens* but could also represent a southern extension of the *H. neanderthalensis* range. The role of Arabia in the early out of Africa dispersals of *H. sapiens* based on stone tool evidence has also been widely discussed (e.g. Armitage et al., 2011;

Rose et al., 2011; Crassard et al., 2013, 2018). A recent fossil finding from the Nefud Desert provided the earliest definitive arrival of *Homo sapiens* by c. 90 ka and indicated that their early dispersals beyond Africa were not restricted to the Levantine woodlands (Groucutt et al., 2018), as suggested elsewhere (Shea, 2008; Mellars et al., 2013). Roberts and Stewart (2018) recently stressed the importance of studies in desert regions (such as Arabia) for elucidating the extent to which our species was unique in its ecological flexibility compared to other non-*H. sapiens* hominins. And although more research is needed, there is some evidence to hint that *H. sapiens* in Arabia were penetrating further into the dune fields and under harsher conditions than their middle Pleistocene predecessors (Breeze et al., 2017; Roberts et al., 2018).

This thesis

The Arabian Peninsula occupies a unique position for shedding light on some of the outstanding questions regarding hominin and faunal evolution and dispersals, namely: when did hominins, and in particular *H. sapiens*, first leave Africa? Did hominins disperse alongside other mammalian fauna? What were the causal mechanisms driving hominin and mammalian dispersals and range expansions? What ecological settings did hominins encounter immediately beyond Africa? And what can this tell us about the ecological flexibility and dispersal capabilities of members of our genus?

To begin to address these questions it is critical that we develop a comprehensive understanding of the faunal (as well as floral) context of hominin dispersals into and occupation of Arabia. Yet, only a handful of palaeontological sites have been reported from the Arabian Peninsula (Thomas et al., 1998; Delagnes et al., 2012) and even fewer have been studied

in detail (Stimpson et al., 2016; Groucutt et al., 2018). To address this, I conduct detailed taxonomic, taphonomic, zooarchaeological, and isotopic analysis of various fossil fauna deposits spanning the middle to late Pleistocene (*Chapters Three* to *Six*).

A primary goal of this thesis is to investigate the influence of changes in mammalian biogeography on hominin distribution, behaviour, and evolution. It is therefore first important that mammalian palaeobiogeography is put into a broader geographical and temporal context. This is the aim of *Chapter Two*, which is published in *Quaternary* International (Stewart et al., 2017). In this chapter I conduct an extensive review of the large mammal fossil record from Arabia and the surrounding regions - East and North Africa, southwest and South Asia. I restrict the review to the past one million years for two key reasons: firstly, unlike earlier periods, no attempts had yet been made to synthesise the mammalian fossil record of the middle and late Pleistocene; and secondly, I consider this to represent an appropriate time-frame for addressing questions regarding hominin incursions into Arabia based on current archaeological data.

As highlight above, climate change was clearly important for hominin dispersals into the region. Despite this, there has been no direct means of determining precisely how climate change affected aridity in the Arabian interior. This has made testing hypotheses regarding the ecological flexibility of hominins moving into the region difficult. In *Chapter Three*, which is published in *Nature Ecology & Evolution* (Roberts et al., 2018), my colleagues and I set out to determine precisely what wetter represents – in terms of rainfall and humidity – in the context of regional ecology. This study was inspired by the discovery of stone tools and possibly butchered bones during renewed investigations of the middle Pleistocene fossil assemblage from Ti's

al Ghadah. This initial discovery was significant in its own right as it represented the oldest directly dated hominin presence in the Arabia Peninsula (c. 500–300 ka), considerably older than the previously oldest site of Jebel Qattar 1 at c. 210 ka (Petraglia et al., 2012). But equally important, these findings provided a unique opportunity to study the immediate ecology associated with this hominin presence. To do so, we conduct stable carbon and oxygen isotope analysis of fossil herbivore teeth to provide insights into regional palaeoaridity and palaeovegetation.

In *Chapter Four*, which is published in *Quaternary Science Reviews* (Stewart et al., 2019), I conduct renewed sedimentological, taxonomic, taphonomic, and zooarchaeological investigations of the Ti's al Ghadah fossil assemblages. Earlier cursory investigations of the Ti's al Ghadah basin identified surface scatters of lithic artefacts and fossils, as well as older and younger phases of lake formation, but it remained unclear how these were stratigraphically related (Scerri et al., 2015; Stimpson et al., 2015, 2016). Elucidating the stratigraphy of the basin and nature of the palaeolake deposits is the first aim of this chapter. Secondly, this study aims to assess which agents(s) were primarily responsible for the accumulation of the fossil assemblages and evaluate evidence outside directly imparted butchery marks that might be consistent with accumulation of fauna by hominins. This study represents one of only two detailed taphonomic analyses of an Arabian fossil assemblage, the other being Al Wusta (Groucutt et al., 2018; see *Chapter Seven*, Appendix A).

As part of the continual effort to collect palaeontological, palaeoenvironmental, and archaeological data, my colleagues and I undertook fieldwork in the western Nefud Desert during January of 2016. This fieldwork involved continued investigations at previously discovered

sites (as in *Chapters Three* and *Four*) and surveying for new sites. One of the newly discovered sites, which was dubbed Alathar (from the Arabic word الأثر meaning "the trace"), is presented in *Chapter Five*. While surveying the site, we quickly observed that the palaeolake deposit was covered in tracks (or footprints) of various mammals, including some clearly identifiable as hominin. The unique setting and taphonomic factors affecting the long-term preservation of tracks means that groups of tracks, and particularly those in similar states of preservation, can be assumed to have been generated in a very short window, usually within a few hours or days (Cohen et al., 1991; Hatala et al., 2016; Roach et al., 2016). As a result, tracks and trackways can provide palaeoecological and behavioural snapshots not afforded by more time-averaged archaeological and fossil assemblages. In this chapter, I present a detailed analysis of the Alathar tracks, fossils, and palaeolake sediments to gain unique insights into hominin and non-hominin mammal palaeoecology and behaviour within the Arabian interior.

The study described in Chapter Six is aimed at elucidating the preservational pathways that bones and fossils in the western Nefud Desert have undertaken. To do so, I conduct a taphonomic analysis of various circum-lacustrine fossils deposits collected from the western Nefud Desert over numerous field seasons. Despite the wealth of actualistic and naturalistic landscape studies within semi-arid grasslands (e.g. Behrensmeyer, 1978; Blumenschine, 1986, 1988; Domínguez-Rodrigo, 1999, 2001; Faith and Behrensmeyer, 2006), very few have been devoted to understanding the taphonomic process operating in desert environments (Andrews and Whybrow, 2005; Denys et al., 2007). It is important that these are considered when working in Arabia, and other similar areas (e.g. the Sahara), where climate has alternated between humid and hyper-arid over

14

millennia, potentially exposing bones and fossils to a suite of environmental conditions and preservation pathways.

The studies in this thesis will build upon recent palaeontological, palaeoenvironmental, and archaeological research that has highlighted the importance of the Arabian Peninsula in the story of hominin prehistory. I will utilise the fossil record to provide unique and detailed insights into the interplay between hominins, animals, and the environment, investigate the unique taphonomic processes involved in the formation and accumulation of fossil assemblages within the Arabian interior, and shed light on broader questions surrounding hominin and fauna evolution and dispersal across continents. Taken together, the studies in this thesis will contribute of important new insights that could help us answer some palaeoanthropology's outstanding questions.

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CHAPTER TWO

Middle and late Pleistocene mammal fossils of Arabia and surrounding regions: Implications for biogeography and hominin dispersals

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Declaration

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Mathew Stewart

ABSTRACT

Plio-Pleistocene faunal turnovers and their implications for hominin dispersals have recently received considerable attention. Exploration and palaeontological study of faunal exchanges has traditionally centred on East Africa, North Africa, and the Levant in Southwest Asia. Despite this attention, considerable debate surrounding the timings, rates, and directions of hominin dispersals remain. Notwithstanding its close geographical proximity to these regions and a landmass of over 3 million km², the Arabian Peninsula has largely been excluded from these discussions, mostly owing to the paucity of its Pleistocene vertebrate record. However, recent palaeoenvironmental studies have demonstrated that Arabia experienced periods of climatic amelioration during the Pleistocene, resulting in the establishment of large, perennial water sources and open-grasslands; conditions vastly different than today. This interpretation is further underpinned by archaeological and palaeontological data, and it is now clear this region is important for understanding faunal and hominin movements between Africa and Eurasia. Examination of the Arabian middle to late Pleistocene fossil record in a biogeographical context indicates the composite nature of the Arabian faunal record, with Eurasian and African intrusions present in addition to well-established endemics. Open grassland habitats and taxonomic similarities between Pleistocene Arabia on the one hand, and the Levant and Africa on the other, suggests that hominin dispersal into Arabia did not require significant behavioural and/or technological innovations, while subsequent climatic deterioration likely resulted in hominin and faunal retreat/extirpation.

INTRODUCTION

Major shifts in biogeography and faunal turnovers during the Pleistocene (2.58 million-years-ago, or Mya, to 11.7 thousand-years-ago, or ka) are usually attributed to significant climate changes, although the importance of biotic interactions (e.g. competition, disease) is becoming increasingly apparent (Tchernov, 1992; Faith et al., 2012; Faith, 2014; Bibi and Kiessling, 2015). Developing a comprehensive understanding of the timing, rates, and directions of migrations, particularly for large mammals, is essential when considering coeval hominin dispersals (Tchernov, 1998; Bobe et al., 2007; Faith et al., 2007). The faunal record also serves as a good indicator of palaeoenvironments that may have hindered or facilitated dispersals (Bobe and Behrensmeyer, 2004; Van der Made, 2011; Lyman, 2017). Despite considerable attention, the nature and extent of faunal and hominin exchanges between Africa and Eurasia is still highly debated (Martínez-Navarro, 2004a; 2010; O'Regan et al., 2005; Belmaker, 2010; Belmaker and O'Brien, 2017). While it is possible that crossing the Red sea at the Bab el-Mandeb provided a dispersal route, particularly during periods of low sea level, no land bridge has been present for millions of years (Fernandes et al., 2006). We therefore emphasise the 'northern route', across the Sinai Peninsula, as the primary connection between African and Eurasia. Notwithstanding its geographical proximity, Arabia has largely been excluded from these discussions owing to a dearth of archaeological and palaeontological research in the region. However, new palaeoenvironmental (Rosenberg et al., 2013; Breeze et al., 2015; 2016; Farrant et al., 2015; Hoffmann et al., 2015; Jennings et al., 2015b; Parton et al., 2015a; 2015b), archaeological (Armitage et al., 2011; Groucutt and Petraglia, 2012; Petraglia et al., 2012; Hilbert et al., 2014; Scerri et al., 2014; 2015; Shipton et al., 2014; Groucutt et al., 2015; 2016; Jennings et al., 2016) and palaeontological

(Stimpson et al., 2015, 2016) studies have begun to shed light on this region, highlighting its importance for a holistic understanding of faunal (including hominin) exchanges between Africa and Eurasia. The importance of Arabia has also been specifically stressed in the study of hominin dispersals (Groucutt et al., 2015b).

Arabia today is characterised by a mosaic of habitats including semi-tropical and montane regions near the southern and western coastal regions, with an interior dominated by vast hyper-arid sand seas – the Nefud, Empty Quarter, and Wahiba sands (Edgell, 2006; Vincent, 2008). However, during the Pleistocene, the Arabian Peninsula was witness to cyclical upturns in humidity and precipitation that led to the activation of rivers, lakes, and the establishment of palaeohydrological corridors, both within and between Arabia, the Levant, and Africa (Breeze et al., 2016). These likely enabled the dispersal of fauna, including hominins, into Arabia and across its interior (Rosenberg et al., 2011; 2013; Groucutt et al., 2015a; Breeze et al., 2016). Fossiliferous and archaeological sites tend to correspond with humid periods (Delagnes et al., 2012; Petraglia et al., 2012; Stimpson et al., 2016), and it is now clear that hominins dispersed into Arabia as early as the middle Pleistocene (Groucutt and Petraglia, 2012; Jennings et al., 2015a; Scerri et al., 2015). Subsequent climatic deterioration likely resulted in faunal retreat, extirpation/extinction, and speciation (e.g. Faith and Behrensmeyer, 2013)

McClure (1984) was the first to report on Pleistocene fossils from Arabia. He collected and identified numerous taxa from lacustrine deposits in the Empty Quarter and suggested that palaeolakes in the region were activated by moderate to heavy summer monsoons and persistent light to medium rainfall throughout the year, permitting expansive grasslands; an interpretation supported by the fauna recovered (e.g. *Bos* and *Hippopotamus*). Furthermore, the presence of hippos is testament to

permanent muddy, fluvial, or lacustrine conditions (Estes, 1991). Radiocarbon dating of shells within marl beds indicate that lake formation occurred between c. 40-20 ka (McClure, 1984). However, recent redating of these lacustrine deposits using optically stimulated luminescence (OSL) dating pushed back the timing of pluvial periods to the early late Pleistocene (c. 80-125 ka; Rosenberg et al., 2011). Thomas et al. (1998) reported three fossiliferous sites from lacustrine deposits in the western Nefud Desert. An early Pleistocene age was originally suggested on the basis of the fauna (Thomas et al., 1998); however, recent direct dating indicated that these localities ranged from the middle to late Pleistocene (Rosenberg et al., 2013; Stimpson et al., 2016). Stimpson et al. (2015; 2016) also reported systematic excavations at Ti's al Ghadah ('Thomas locality-2') that yielded an abundance of well-preserved fossils, including the first Pleistocene-aged birds identified in Arabia. The palaeoecology of fossil taxa present at Ti's al Ghadah are strongly suggestive of a more humid climate and greater water availability than what prevails today (Stimpson et al., 2015; 2016). Specifically, the presence of hippopotamids, fish, and birds with strong affinities toward water (e.g. Anas, Tachybaptus) are testament to large, perennial water sources; while the presence of alcelaphines, Equus hemionus, and Pelorovis suggest expansive grasslands (Breeze et al., 2017). Productive grasslands during the middle Pleistocene are supported by high ¹³C values obtained for herbivore teeth (Thomas et al., 1998) and dental mesowear patterns of Palaeoloxodon (Stimpson et al., 2016). There appears to be a positive correlation between Oryx spp. body size and rainfall, and thus, the large Oryx remains from Ti's al Ghadah relative to the smaller extant endemic O. leucoryx may suggest greater water availability during the formation of this site (Stimpson et al., 2016). Finally, the presence of large herbivores (Palaeoloxodon) and large carnivores (Panthera gombaszogensis) suggest that, at times during the Pleistocene, the western Nefud Desert boasted environments that could

support a substantial biomass (Stimpson et al., 2016). Delagnes et al. (2012) reported a late Pleistocene fossil bearing site approximately 50 km from the western coast of Yemen. Unfortunately, a significant portion of the fossil material recovered was poorly preserved, and taxonomic identifications were mostly only possible to family level. Thus, little can be said regarding the late Pleistocene palaeoenvironments based on these fossils. Nonetheless, tentatively assigned remains of *E. hemionus* were identified, suggestive of an arid steppe environment (Delagnes et al., 2012).

In order to elucidate the nature of faunal incursions into the Peninsula, we review mammalian taxa recovered from major fossiliferous deposits from Arabia and surrounding regions. First, it important to provide operating definitions for the common habitat types mentioned here, and elsewhere in this thesis. Savannas, which are often associated with early hominin occupation and dispersals (see Chapter One), comprise a multitude of habitats ranging from grasslands, shrublands, bushlands, and woodlands, and some have argued that the term is impractical and too often uncritically applied to discussion of hominin palaeoecology (Reed and Rector, 2006). Here, savannas are defined as "mixed tree-grass systems characterized by a discontinuous tree canopy in a continuous grass layer" (Ratnam et al., 2011: p. 653) and use it to describe the broad environmental setting occupied by some hominins. However, some more practical habitat types are used throughout this thesis, and warrant definition here: grasslands, characterised by abundant grasses and limited to no tree cover; shrublands, receive limited rainfall and are dominated by small shrubs/trees (1–3 in height) and some seasonal grasses; bushlands, receive greater rainfall than shrublands (~250–600 mm/year) and are characterised by taller tree and bush communities; woodlands, higher rainfall still (~600-1000 mm/year) and with larger, more densely populated trees; forests, receive high amounts of rainfall, have densely populated tree communities with interlacing canopies, multiple overlapping vegetative strata, and ground cover characterised by ferns and epiphytes, as opposed to woodlands in which ground cover is dominated by grasses; and deserts, which receive very little rainfall and are characterised by drought tolerant plants (White et al., 2000; Reed and Rector, 2006). Moreover, terms such as open, intermediate, and closed are often used in conjunction with these habitats types to indicate the degree of cover (sometimes expressed as a percentage) – for example, open and closed woodlands refer to those in which trees are sparsely and densely populated, respectively.

Secondly, and as stressed by Belmaker (2017a), it is important to clearly define/delineate the regions examined. Politically defined areas often have no bearing on palaeontological studies, and regions derived from species distributions and phylogenetic relationships are far more suitable (Belmaker, 2017a). For these reasons, we used the non-marine mammal biogeographic realms and regions described by Holt et al., (2013; Fig. 4D and S4C; see Figure 1 for region definitions), although it is acknowledged that these are based on modern data and are not perfect analogues for the Pleistocene. While South Africa is not a focus of the present review, we do provide some reference to the South African fossil record where we believe it helps contextualise the fossil record of Africa and elsewhere. This review is focused on ungulates, proboscideans, and carnivores, all of which have been recorded in the Arabian Pleistocene fossil record and are known to significantly impact human behaviour (Belmaker, 2017b; Lewis, 2017; Madurell-Malapeira et al., 2017). We restrict this review to the middle and late Pleistocene, although the late early Pleistocene (c. 1.2–0.7 Ma) is also considered following Potts and Deino (1995) to capture changes associated with the middle Pleistocene transition (MPT; c. 780 ka). This review is presented in three sections: 1) origins of taxa and earliest occurrences in Arabia, general ecology, and middle Pleistocene distribution; 2) late Pleistocene distributions; and 3) a discussion of major palaeobiogeographical trends, connections between Arabia and Africa/Eurasia, and implications for hominin dispersals into Arabia.

MIDDLE PLEISTOCENE FAUNA AND ITS BACKGROUND

Suidae

Pigs have their origins in Eurasia and likely migrated into Africa during the earliest Miocene, after which the family underwent significant radiation, especially in the Pliocene (Bishop, 2010). During the middle Pleistocene, Africa was home to a diverse and abundant suid fauna. Common around the MPT in Africa were members of Kolpochoerus (K. limnetes, K. majus and K. olduvaiensis) and Metridiochoerus (M. compactus, M. modestus and *M. hopwoodi*). Kolpochoerus dispersed from Africa reaching as far north as Evron Quarry, Israel, where an endemic form, K. evronensis, occurred (Tchernov et al., 1994). However, Martinez-Navarro (2004) mentioned that this genus dispersed into South Asia during the early Pleistocene, and therefore its presence in the Levant may represent a dispersal from the Oriental. An apparent turnover in the African suids occurred between 400-600 ka with the extinction of Kolpochoerus and Metridochoerus and first occurrence of the extant *Phacochoerus aethiopicus* and *Potamochoerus porcus* - although, recent excavations on Rusinga Island, Kenya, dated to the late Pleistocene, unexpectedly yielded *Kolpochoerus* remains that closely match K. majus (Faith, 2014).



Figure 1. Map of major sites referred to in the text. 1 Lake Eyasi, Mumba Shelter; 2 Olduvai; 3 Lainyamok; 4 Olorgesailie; 5 Lukenya Hill; 6 Isenya; 7 Kanjera; 8 Kapthurin (K3); 9 Omo, Kibish Formation; 10 Gombore II; 11 Aduma; 12 Bodo mbr, Meadura mbr, Dakanihyalo mbr, Bouri-Daka; 13 Asbole; 14 Hara Idé; 15 Buia; 16 Bir Tarfawi; 17 Sodmein Cave; 18 Haua Fteah; 19 El Guettar Cave; 20 Sidi Zin; 21 Tighenif (formerly Ternifine); 22 Rhafas Cave; 23 Jebel Irhoud; 24 Oulad Hamida 1 (OH1; formerly Thomas Quarry 3), Thomas Quarry 1 (Th1); 25 Sidi Abderrahmae; 26 Aïn Bahya; 27 Doukkala II; 28 Salé; 29 El Harhoura 2 Cave; 30 Ain Maarouf; 31 Mugharet el 'Aliya; 32 Abu Noshra; 33 Ti's al Ghadah, Khall Amayshan-1; 34 Shi'bat Dihya; 35 Empty Quater; 36 Revadim Quarry; 37 Nahal Agev; 38 Umm Qatafa; 39 Holon; 40 Qesem Cave; 41 Kharaneh IV; 42 Shishan Marsh; 43 Kebara Cave; 44 Tabun Cave; 45 'Ubeidiya; 46 Geula Cave, Sefunim Cave; 47 Qafzeh; 48 Gesher Benot Ya'agov; 49 Amud Cave; 50 Hayonim Cave; 51 Evron Quarry; 52 Ksar 'Akil; 53 Yabrud Shelter; 54 Douara Cave; 55 Umm el Tlel; 56 Nadaouiyeh Aïn Askar; 57 Latamne; 58 Dederiyeh Cave; 59 Emirkaya; 60 Dursunlu; 61 Denzili; 62 Yarimburgaz Cave; 63 Shanidar; 64 Akhalkalaki; 65 Wezmeh Cave; 66 Kaldar, Yaftzeh Cave; 67 Qalehjough; 68 Lakhuti; 69 Tepke; 70 Locality 642, Locality 73, Locality 362; 71 Sardhok; 72 Dhasan River; 73 Bhagalpur; 74 Gopnath; 75 Hathnora; 76 Teggihali; 77 Billasurgam Caves, Chintamani Gavi, Charnel Cave, Cathedral Cave; A. Ganga Valley; B. Son Valley; C. Narmada Valley; D. Godavari Valley; E. Manjra Valley; F. Ghod Valley. Regions were selected based on the non-marine mammal zoogeographic regions described in Holt et al. (2013; Fig. 4D and S4C). These regions are numerically denoted [for region numbers see Holt et al. (2013; Fig. S4C)] and consequently for ease of reading, and to assist in describing trends in biogeography, cross-taxon realm and directional terminology with respect to site locality is used to distinguish regions (Holt et al. 2013; Fig. S1). The regions considered here are as follows: eastern Afrotropical (light blue), Saharo-Arabian (red), northern Saharo-Arabian (purple), eastern Saharo-Arabian (brown), Palearctic (green), and Oriental (yellow). Despite the eastern Afrotropical region extending to the west coast, the terminology applied here was selected based on the restriction of sites to East Africa. Dashed lines in the Oriental region represent subregion boundaries outlined in Holt et al. (2013; Fig. S4C).
In the eastern Afrotropical region, *Phacochoerus aethiopicus* and Potamochoerus porcas are first recorded at Kapthurin (McBrearty et al., 1996), although there is an earlier report of *Phacochoerus* sp. at Kanjera North (Ditchfield et al., 1999). Contemporaneously, northern Saharo-Arabia saw the arrival of *Phacochoerus* sp. cf. *Ph. africanus* at Thomas Quarry 1 (Th1-G) and Oulad Hamida 1 Rhino Cave, Morocco (OH1-GDR; Geraads 2002). A single occurrence of Sus sp. cf. S. strozzi is reported in Turkey (Gulec et al., 2009), and S. scrofa is present in the Palearctic and eastern Saharo-Arabian regions of the Levant (Marder et al., 1999; Rabinovich and Biton, 2011; Rabinovich et al., 2012). Two unidentified suid specimens were reported from Locality 642 and Locality 73 from the Upper Siwaliks, Pabbi Hills, Pakistan (Dennell et al., 2005a; 2005b). Species of Sus dispersed from Eurasia into northern Saharo-Arabia during the second half of the middle Pleistocene, as evidenced by occurrences at Doukkala II (Michel and Wengler, 1993). In eastern Saharo-Arabia, suids appear restricted to the western most regions and no remains are known from the Arabian Peninsula during the middle Pleistocene.

Hippopotamidae

Hippos evolved in East Africa with their earliest appearance during the Miocene (Weston and Boisserie, 2010). They are known from the late Miocene Baynunah Formation, United Arab Emirates (UAE; Bibi et al., 2013). Modern hippopotamids are represented by two extant species, *Hippopotamus amphibius* and the pygmy *Choeropsis (Hexaprotodon) liberiensis*. The presence of hippos is a useful indicator of nearby large, permanent water bodies (Eltringham, 1999; Weston and Boisserie, 2010). The biogeographical history of *Hippopotamus* is complex and involves numerous out-of-Africa dispersals during the Plio-Pleistocene, resulting in speciation events that gave rise to species in Europe (H. antiquus), East and South Africa (*H. gorgops*), North Africa (*H. sirensis*), and the Levant (*H. behemoth*) (O'Regan et al., 2005; Pushkina, 2007; Belmaker, 2010). However, some researchers have suggested, based on an overlap in size, that H. behemoth and *H. gorgops* represent a single species (Martínez-Navarro, 2010). Speciation was likely the result of habitat fragmentation (widening of distances between suitable water bodies) that restricted latitudinal dispersal between populations (Belmaker, 2010; Weston and Boisserie, 2010). Hippopotamus amphibius was the most common and widespread hippopotamid in the middle Pleistocene, particularly so in East Africa and in the Palearctic regions of the Levant, and has been found as far east as Georgia (Hemmer et al., 2001). The extinction of H. gorgops appears to occur around the MPT, with late appearances reported at Olduvai Bed IV (Leakey and Roe, 1994), Kanjera North (Ditchfield et al., 1999) and Olorgesailie member 10 (Koch, 1986; Potts, 1989). Likewise, the North African endemic, H. sirensis, appears to go extinct around this time (or shortly after), as recorded at Tighenif, Th1-G, and Ain Maarouf (Geraads, 2002). *Hippopotamus behemoth* remains were found at 'Ubeidiya (Tchernov et al., 1994), and tentatively assigned remains were also identified at Latamne (Guérin et al., 1993), the latter indicating a possible synchronous extinction with the African endemics. As noted by O'Regan et al. (2011), the dispersal of Hippopotamus further east into the Oriental region may have been hindered by the presence of the already established *Hexaprotodon*, a genus that survived until the late Pleistocene in Asia (Louys et al. 2007; Boisserie 2005 and references therein). Remains of Hex. ("Hip.") namadicus are known from India and Pakistan and have been identified at Hathnora (Sonakia and Kennedy, 1985), Lower Narmada (Joshi et al., 1982), and Sardhok (Siddiq et al., 2016). Interestingly, remains of *Hexaprotodon* sp. were identified in Eritrea c. 1.0 Ma, far younger than other findings from this region (Martínez-Navarro, 2004b). Species of Hippopotamidae have not yet been reported from eastern Saharo-Arabia during the middle Pleistocene.

Camelidae

Camels migrated into Africa from Eurasia with their earliest appearances in Chad around the terminal Miocene (Harris et al., 2010). Despite their long-standing presence in Africa, the camelid record is scant and its Pleistocene biogeography is poorly understood. The scarcity of fossils may be the result of the destructive forces of arid environments, conditions for which camels are particularly well-adapted. During the middle Pleistocene, camels were abundant in the Levant (Guérin et al., 1993; Tchernov et al., 1994; Reynaud Savioz and Morel, 2005; Nowell et al., 2016). Palearctic remains of *Camelus thomasi* have been identified in Syria at Nadaouiyeh Aïn Askar (Reynaud Savioz and Morel, 2005) and as far east as Lakhuti-2 (Sotnikova et al., 1997), while remains from Africa have been reported from Tighenif in Algeria (Geraads et al., 1986; Geraads, 2012), and Bir Tarfawi in Egypt (Wendorf et al., 1993). In Saudi Arabia, a poorly preserved maxilla of a camelid was reported from Ti's al Ghadah (Thomas et al., 1998).

Giraffidae

While restricted to Africa today, during the Mio-Pliocene giraffids were abundant in Eurasia and have been recorded in early and late Miocene deposits in eastern Saudi Arabia (Thomas et al., 1982; Bibi et al., 2013). Large, heavily built sivatheres are known from Arabia, the Siwaliks of Pakistan, and India, and Turkey (Harris and Solounias, 2010), as well as African deposits as young as c. 0.78 Ma (Leakey and Roe, 1994; Asfaw et al., 2002). Roughly contemporaneous is the extinction of *Giraffa jumae* and *G*. gracilis in the East Africa (Leakey and Roe, 1994; Martínez-Navarro, 2004b; Gallotti et al., 2010). Both *G. gracilis* and *G. jumae* are suspected ancestors of the extant *G. camelopardalis* (Mitchell and Skinner, 2003), which first appeared in Africa *c.* 1 Ma at Bouri-Daka, Ethiopia (Asfaw et al., 2002). The only middle Pleistocene non-African occurrences of *G. Camelopardalis* were at Latamne, Syria (Guérin et al., 1993), and unidentified giraffid remains have been recovered at Dursunlu, Turkey (Gulec et al., 2009) and 'Ubeidiya, Israel (Tchernov et al., 1994). As suggested by Belmaker (2010), Eurasian giraffids during the Pleistocene may represent relic Pliocene populations of *Giraffa* and not a dispersal event from Africa.

Bovidae

The earliest "bovid-like dental remains" are known from the Oligocene in Mongolia (Gentry, 2010a, p. 744). During the Miocene, bovids underwent a significant adaptive radiation under a backdrop of increased aridity and expansion of open grasslands (Tchernov, 1992). This is reflected by increases in body size, dental hypsodonty, and lengthening of limbs adapted for cursorial locomotion, traits that are beneficial to bovids in open-grassland habitats (Bobe and Behrensmeyer, 2004). Bovids first appear in Arabia and Africa during the early Miocene following the closure of the Mediterranean/Indo-Pacific seaway and the establishment of a land bridge connecting Eurasia with Arabia and Africa (Thomas et al., 1982; Tchernov, 1992; Gentry, 2010a). Thomas et al. (1982) identified late Miocene bovid horncore and dental remains, similar in size to Gazella dorcas, in eastern Saudi Arabia, and numerous bovid taxa are known from the late Miocene Baynunah Formation of the UAE (Bibi et al., 2013).

Hippotraginae

Hippotraginae are particularly well-adapted to arid conditions and are first found in Chad c. 7 Ma (Bibi et al., 2009). Hippotragines are mostly restricted to Africa, but Plio-Pleistocene remains have been found in the Siwaliks of Pakistan (Patnaik, 2013), and Oryx is known from the middle Pleistocene at Nadaouiyeh Aïn Askar, Syria (Reynaud Savioz and Morel, 2005), and Ti's al Ghadah, Saudi Arabia (Thomas et al. 1998; Stimpson et al. 2015, 2016). Specimens attributable to Oryx and other ungulates of similar size dominate the Ti's al Ghadah faunal record. Both Thomas et al. (1998) and Stimpson et al. (2016) noted that the dental morphology of the Ti's al Ghadah Oryx most closely resembles that of extant desert-adapted forms (O. dammah and O. leucoryx), but differ from all modern species in horn core divergence. Stimpson et al. (2016) suggested, based on their comparatively large size, that the Ti's al Ghadah Oryx represents a larger-bodied extinct form of the extant O. leucoryx. The extant O. beisa and O. gazella are known throughout the middle Pleistocene in Africa (Geraads et al., 1986; Mehlman, 1987; Potts and Deino, 1995; Amani and Geraads, 1998; McDougall et al., 2005; Faith et al., 2012; Geraads, 2012). Hippotragus equinus is first reported in the eastern Afrotropical region at Lainyamok (Potts and Deino, 1995; Faith et al., 2012). The extinct H. gigas is known from African Saharo-Arabia from the early middle Pleistocene (Geraads et al. 1986; Geraads 2012; Martínez-Navarro, 2004b).

Alcelaphinae

Alcelaphinae are well adapted to open-grasslands, as evidenced by their highly hypsodont teeth and cursorial limbs (Bobe and Behrensmeyer, 2004). They are first known from the late Miocene of Africa and Europe, and from the Pliocene in India; however, there is some doubt surrounding the identification of the European remains (Gentry, 2010a). During the middle Pleistocene, alcelaphines were diverse and abundant in Africa, and present but rare in Eurasia. An apparent turnover in alcelaphines occurred following the MPT, with the extinction of Megalotragus kattwinkelli, Parmularius angusticornis, and P. rugosus, and the subsequent appearance of Alcelaphus buselaphus in East Africa at Kapthurin (McBrearty et al., 1996) and Bodo member (Kalb et al., 1982). Alcelaphus buselaphus first appears in the northern Saharo-Arabian region c. 400ka at Doukkala II (Michel and Wengler, 1993), having likely migrated from around the Horn of Africa. Connochaetes taurinus is common throughout the middle Pleistocene in both the Afrotropical and Saharo-Arabian regions of Africa. Damaliscus niro disappears from East Africa sometime during the middle Pleistocene, but is survived by representatives in the southern Afrotropical region (de Ruiter et al., 2008). Lainyamok yielded an additional three alcelpahine species -D. hypsodont, D. lunatus, and Beatragus hunteri (Potts and Deino, 1995; Faith et al., 2012). A single occurrence of *Damalops palaeindicus* was reported from Locality 642, Upper Siwaliks, Pakistan (Dennell et al., 2005b), and an unidentified alcelaphine species from Locality 610, India (Dennell et al., 2006). Thomas et al. (1998) noted that isolated upper and lower molars recovered from Ti's al Ghadah in Saudi Arabia likely represent an alcelaphine.

Antilopinae

Many members of Antilopinae have highly hyposodont teeth and cursorial limbs suggesting an affinity toward arid and open grasslands (Bobe and Behrensmeyer, 2004). They are first known from the middle Miocene in Eurasia and Africa (Gentry, 2010a). During the middle Pleistocene, antilopines were highly abundant and diverse. Common in East Africa were *Eudorcas thomsoni* and *Nanger granti*, both of which have been recorded at Asbole (Geraads et al., 2004) and Lainyamok (Potts and Deino, 1995; Faith et al., 2012). In general, the African Saharo-Arabian antilopine record consists of fewer extant taxa, especially during the early middle Pleistocene, during which the North African extinct endemic *Gazella atlantica* dominates. By the mid-middle Pleistocene modern forms appear as represented by *G. dorcas* and *G. cuvieri*. The Palearctic, Oriental, and eastern Saharo-Arabian antilopine record consists of entirely extant species and is dominated by *G. gazella* and *G. subgutturosa*. In Saudi Arabia, Thomas et al. (1998) noted that a single spiralled horn core from Ti's al Ghadah may be attributable to Antilopini and most closely resembled remains of antelope recovered from Laetoli, Olduvai, and Omo.

Neotragini consists of African antelopes smaller than *Gazella*, although they may occur in Europe and in the Baynunah Formation in the UAE during the late Miocene (Gentry, 2010a; Bibi et al., 2013). Tentatively assigned remains of *Madoqua* sp. cf. *M. kirkii* were found at Omo Member I (Assefa et al., 2008). Additional unidentified remains of *Madoqua* sp. and *Ourebia* sp. have been reported from mid-late middle Pleistocene sites in the eastern Afrotropical region (Potts and Deino, 1995; McBrearty et al., 1996; McDougall et al., 2005; Faith et al., 2012).

Reduncinae

Members of Reduncinae have a strong affinity for water and typically inhabit marshes and floodplains (Kingdon, 1997). Reduncines are known from the Miocene in Africa and the Siwaliks in Pakistan (Gentry, 2010a; Bibi, 2011); however, during the middle Pleistocene their distribution is limited to Africa and mostly south of the Sahara. The extinct *K. sigmoidalis* was identified at Bouri-Daka, Ethiopia (Asfaw et al., 2002), and the extant *K*. ellipsiprymnus and K. kob are common throughout the middle Pleistocene in eastern Afrotropical. Interestingly, K. ellipsiprymnus reappears c. 400–600 ka in East Africa at Meadura member (Kalb et al., 1982) and Kapthurin (McBrearty et al., 1996) after a long absence. Remains of *Redunca* and *Kobus* have been identified from the early to mid-middle Pleistocene in the northern Saharo-Arabian region of Morocco (Freeman, 1975; Geraads et al., 1986; Michel and Wengler, 1993; Geraads, 2012). No reduncine remains have been recovered from middle Pleistocene eastern Saharo-Arabian.

Tragelaphinae

Tragelaphinae are well-represented in East Africa, poorly in northern Saharo-Arabian, and absent outside Africa. *Tragelaphus scriptus* is ubiquitous throughout the eastern Afrotropical region during the middle Pleistocene. Similar to *K. ellipsiprymnus*, *Tr. strepsiceros* was present during the early middle Pleistocene, followed by a long absence, until its reappearance during the late middle Pleistocene at Omo Member I (Assefa et al., 2008) and Sodmein Cave (Moeyersons et al., 2002). A North African endemic, *Tr. algericus*, was found at Tighenif (Geraads et al., 1986; Geraads, 2012). *Taurotragus*, the largest of the antelopes, is a geologically young genus and may not have appeared until the start of the Pleistocene (Gentry, 2010a). *Taurotragus oryx* is first reported at *c.* 400 ka at Doukkala II in Morocco (Michel and Wengler, 1993) and Lainyamok in Kenya (Faith et al. 2012; Potts & Deino 1995).

Bovinae

Bovinae inhabit a suite of habitats from grasslands (*Bos*) to wetlands and swamps (*Bubalus*). The earliest bovine remains are from the Siwaliks, India, and dated to *c*. 8–9 Ma (Bibi, 2007). The first non-Oriental occurrences

are noted from the UAE and Kenya and dated to c. 8-6 Ma (Bibi, 2007). During the early and middle Pleistocene, there exists a clear distinction between the Africa and Eurasian bovine, with Africa dominated by members of *Pelorovis* and Eurasia dominated by members of *Bison* and *Bos. Pelorovis* antiquus is abundant in East Africa and known from OH1-GDR (Geraads, 2002) and Doukkala II (Michel and Wengler, 1993) in Morocco. Non-African occurrences of P. antiquus (taxonomic nomenclature following Gentry and Gentry, 1978) are noted at 'Ubeidiya (Tchernov et al., 1994). Pelorovis oldowayensis is restricted to Africa and its extinction likely occurred around the MPT with late occurrences at Gombore II, Ethiopia (Gallotti et al., 2010), and Kanjera North, Kenya (Ditchfield et al., 1999). A single occurrence of Bos sp. cf. B. bubaloides from Tighenif, Algeria, may actually be P. oldowayensis (Martínez-Navarro and Rabinovich, 2011), and therefore contemporaneous with extinction in East Africa. Bos and Bison are generally associated with Eurasia; however, the former is recorded at numerous sites in Africa and dispersed as far south as Ethiopia (Geraads et al., 2004). In the Levant there is a shift from a Bison-dominated early middle Pleistocene to a Bos primigenius dominated fauna during the latter stages of the middle Pleistocene. Bos primigenius, the ancestral progenitor of domestic cattle, is thought to have evolved from Bison (or Leptobos), which could explain the apparent replacement in the Levant; although, noteworthy is the early occurrence of Bos primigenius at the early Pleistocene site Evron Quarry, Israel (Tchernov et al., 1994). Conversely, cranial morphology suggests Pelorovis may have been the ancestor of Bos (Martínez-Navarro et al. 2007, although see Gentry 2010). This would suggest an African origin for Bos and subsequent northward dispersal into Eurasia or dispersal of Pelorovis into Eurasia and subsequent evolution of Bos. Tentatively assigned remains of Bos sp. cf. B. primigenius are known from the early middle Pleistocene in Turkey (Stiner et al., 1996; Gulec et al., 2009) and the Indian subspecies, Bos

primigenius namadicus, from Lower Narmada, India (Joshi et al., 1982). Boselaphus sp. is reported from Cathedral Cave, India (Roberts et al., 2014), and both Hemibos sp. and Proamphibos sp. are known from the Upper Siwaliks in Pakistan (Dennell et al., 2005b; Siddiq et al., 2014). In the eastern Saharo-Arabian region, Bos primigenius is known from numerous sites but appears restricted to the Levant (Marder et al., 1999; Reynaud Savioz and Morel, 2005; Rabinovich et al., 2012; Nowell et al., 2016). Numerous specimens of a large bovid were reported by Thomas et al. (1998), although from which locality remains unclear. Nonetheless, at least one specimen is definitely from "Thomas loc-3". Thomas et al. (1998) noted that the derived structure of the P₄ and the mandible differs from Bubalus and Bos primigenius and the dimensions of the molar tooth row and astragalus are comparable to Pelorovis. Also noted is the oval cross-section of two horn core specimens that more closely resemble P. oldowayensis than P. antiquus. However, the late age of this specimen is more suggestive of P. antiquus.

Caprinae

Caprinae likely evolved in the Mediterranean during the Miocene and are mostly restricted to Eurasia. Remains of "caprin or caprin-like taxa" (Bibi 2011, p. 5) have been found in Africa from as early as the Pliocene, but are mostly restricted to the Palearctic realm (Martínez-Navarro 2004; Gentry 2010; Bibi et al. 2009; Bibi 2011 and references therein). *Capra aegagrus* – the ancestor of the domestic goat – is known from the eastern Saharo-Arabian (Marder et al., 1999) and the Palearctic regions (Stiner et al., 1996; 2009; Stiner, 2005). *Capra ibex* was found at Umm Qafata, Israel (Vaufrey 1931, 1951 in Hooijer 1961), and Yarimburgaz Cave, Turkey (Stiner et al., 1996), and an unidentified *Capra* sp. from Alkhalkalaki, Georgia (Hemmer et al., 2001). Remains of *Rupicapra rupicapra* and *Capra caucasica* were found at Kudaro I in Georgia (Baryshnikov, 2002).

Cervidae

Cervidae evolved in Eurasia during the Miocene and are mostly restricted to the region during the middle Pleistocene (Gentry, 2010b). The only middle Pleistocene African occurrence of Cervus is recorded at Doukkala II, Morocco (Laquay, 1986); however, its provenance is doubtful (Geraads, 2012). The bovid/cervid divide marks perhaps the greatest disparity between the African and Eurasian large mammal faunal record. It is possible that competitive exclusion between cervids and bovids hindered dispersal of both groups between continents (Belmaker, 2010). The middle Pleistocene Eurasian cervid record is dominated by extant taxa. Extinct forms include remains of the giant Megaceroides (Praemegaceros) verticornis from the Palearctic (Tchernov, 1992; Guérin et al., 1993; Hemmer et al., 2001) and Cervus punjabicus and Axis cf. sp. A. punjaniensis remains from the Upper Siwaliks, Pakistan (Dennell et al., 2005b; Ghaffar et al., 2017). Both Cervus elaphus and Dama mesopotamica are common throughout the Palearctic during the middle Pleistocene, specifically in the Levant. Capreolus capreolus is known from the Palearctic (Vaufrey 1931, 1951 in Hooijer, 1961; Marín-Arroyo, 2013) and eastern Saharo-Arabian regions (Marder et al., 1999), but like Bos is restricted to the Levant during the middle Pleistocene. The Oriental endemics, Axis axis and Muntjacus sp., were reported from Cathedral Cave, India (Roberts et al., 2014), and Alces alces from Kudaro I, Georgia (Baryshnikov, 2002).

Rhinocerotidae

During the Miocene rhinos underwent significant diversification and are well-known in Eurasia and Africa, with at least four genera recorded from Kenya alone during this time (Geraads, 2010b). They are also known from early and late Miocene deposits in eastern Saudi Arabia and the UAE (Thomas et al., 1982; Bibi et al., 2013). By the early late Pleistocene in Africa, this number declined to two species, represented by the extant Ceratotherium simum and Diceros bicornis, the former being very common. The only other rhino to occur in Africa were migrants from Eurasia - Stephanorhinus (Dicerorhinus) hemitoechus and S. kirchbergensis, and their presence in Africa appears to be ephemeral (Michel & Wengler 1993). Both species are ubiquitous throughout the Levantine middle Pleistocene and the primitive S. etruscus was found at 'Ubeidiya, Israel (Tchernov et al., 1994), and Akhalkalaki, Georgia (Hemmer \mathbf{et} al., 2001). The only eastern Saharo-Arabian remains are that of Dicerorhinus hemitoechus from Nadaouiyeh Aïn Askar (Reynaud Savioz and Morel, 2005) and tentatively assigned remains at Shishan Marsh (Nowell et al., 2016).

Equidae

Horses are known from as early as the Eocene in Europe and North America (MacFadden, 2005) and the three-toed hipparionine horses are known from Arabia during the early Miocene at the Baynunah Formation in the UAE (Bibi et al., 2013). Hipparionine horses first arrived in Africa around the early Miocene and were present up until the middle Pleistocene, as evidenced by a late occurrence at Bodo member, Middle Awash, Ethiopia (Kalb et al., 1982) and Masek Beds, Tanzania (Leakey and Roe, 1994). *Hipparion* is absent from Saharo-Arabian region during the middle Pleistocene but is known from earlier in the Pleistocene (Eisenmann and Geraads, 2007). Notwithstanding this, there is great debate surrounding equid phylogeny, and some researchers have suggested that *Hipparion* is absent from Africa altogether (Bernor et al. 2010, and references therein). *Equus* likely migrated to Africa from Eurasia sometime around the Plio-Pleistocene, taking advantage of the expansion of grasslands, and is first reported in the Shungura Formation, Ethiopia, c. 2.3 Ma (Lindsay et al., 1980; Bobe and Behrensmeyer, 2004). The extinct E. oldowayensis is last reported at Olduvai Bed IV (Leakey and Roe, 1994) and Olorgesailie (Koch, 1986; Potts, 1989) in eastern Afrotropical. The North African endemic, E. mauritanicus is common in the Maghreb. Extant equids, E. quagga ("E. burchelli") and E. grevyi, are known from the late early Pleistocene in eastern Afrotropical but are absent during first half of the middle Pleistocene until their reappearance at Lainyamok, Kenya, c. 400 ka (Potts and Deino, 1995; Faith et al., 2012). Although E. greyvi is mostly restricted to East Africa, Kingdon (1997) suggests that they once ranged from South Africa to China. The Palearctic and eastern Saraho-Arabian regions are dominated by wild asses, namely E. hemionus (Porat and Ronen, 2002; Reynaud Savioz and Morel, 2005; Marín-Arroyo, 2013), but extinct species are also abundant, particularly in the Oriental region (Joshi et al., 1982; Sotnikova et al., 1997; Hemmer et al., 2001; Dennell et al., 2005a; 2005b; Erten et al., 2005; Gulec et al., 2009). In Saudi Arabia, Thomas et al. (1998) reported maxilla, metapodials, and astragalus remains of a large equid, similar in form to remains from Olduvai bed IV (dated c. 1.4 Ma), from the Western Nefud, although from which of the three locations the authors described remains unclear. Stimpson et al. (2015, 2016) uncovered numerous well-preserved equid cranial and post-cranial remains from Ti's al Ghadah. The mandible with a complete M_2 and near-complete M_3 belongs to *E*. hemionus, and the occlusal surface dimensions suggests that it belongs to a large form, likely E. h. hemionus or E. h. kiang (Stimpson et al., 2016).

Proboscidea

Proboscideans are a highly speciose group and their biogeographical history involves numerous dispersal events out of Africa, dispersals back into Africa, and dwarfing events (Azzaroli et al., 1988; Todd, 2010). At least three groups of proboscideans are known from Arabia during the Miocene -Deinotheridae, Gomphotheriidae, and Elephantidae (Thomas et al., 1982; Bibi et al., 2013). Palaeoloxodon (Elephas) recki is ubiquitous in East Africa throughout the early to mid-middle Pleistocene and last occurrences are noted c. 400–600 ka in the Bodo member, Meadura member, and Dakanihyalo member, Middle Awash, Ethiopia (Kalb et al., 1982). The dispersal of P. recki out of Africa c. 2.5 Ma resulted in the evolution of P. antiquus, a species commonly known from the Palearctic during the Pleistocene (Martínez-Navarro, 2010; Todd, 2010). The out of Africa dispersal of *Elephas* is thought to have occurred c. 3.7 Ma, resulting in the evolution of the Asian elephant, Elephas maximus (Todd, 2010), a species that is abundant throughout the Plio-Pleistocene deposits of the Siwaliks in India (Patnaik, 2013). Elephas iolensis, a Eurasian migrant to Africa, is known from northern Saharo-Arabian region (Freeman, 1975; Geraads, 2002). Loxodonta atlantica - the ancestral progenitor of the extant Loxodonta africana - is well-known from the northern Saharo-Arabian and its extinction likely occurred c. 400 ka (Freeman, 1975; Geraads et al., 1986; Geraads, 2002; 2012). Loxodonta africana first appeared in the eastern Afrotropical region during the early middle Pleistocene at Kanjera North (Ditchfield et al., 1999), and possibly in the Saharo-Arabian at the Wehaietu Formation, Awash, Ethiopia (Kalb and Mebrate, 1993), but fossil remains are scant throughout the middle Pleistocene. In addition to members of *Palaeoloxodon* and *Elephas*, Eurasia is characterised by the presence of Stegodon and Mammuthus. Stegodon trogontherii is know from numerous sites in the Palearctic (Hemmer et al., 2001; Gulec et al., 2009; Guérin et al., 1993). In eastern Saharo-Arabia, Thomas et al. (1998, p. 148) "very tentatively" assigned elephant remains found at Ti's al Ghadah to P. ("E.") recki based on carpal and tarsal morphology that differed from the extant African forms. Further excavations at Ti's al Ghadah by Stimpson et al. (2015, 2016) uncovered additional elephant remains. Comparative morphometric analyses revealed that the specimens most closely resemble *P. recki* and *P. antiquus*, and as the morphometry falls within the range of both, Stimpson et al. (2016) agreed with Thomas et al.'s (1998) identification of *Palaeoloxodon* sp. cf. *P. recki*. If correct, the Arabian remains would represent one of the youngest occurrences of *P. recki*. Remains of *P. antiquus* have also been reported from Revadim, Israel (Marder et al., 1999).

Hyaenidae

Species of Hyaenidae widely dispersed were during the Plio-Pleistocene, with extant members, Crocuta crocuta and Hyaena hyaena, known from as early as the late Pliocene (Werdelin and Peigné, 2010). The large, robust Pachycrocuta brevirostris is last reported from the Oriental region c. 1.2 Ma at Locality 642 and Locality 73 (Dennell et al., 2005a; 2005b), in Africa c. 1.0 Ma at Bouri-Daka, Ethiopia (Asfaw et al., 2002), but appears to have persisted in the Palearctic until the early middle Pleistocene as evidenced by remains at Lakhuti-2, Tadjikistan, and Tepke-2, Kyrgyzstan (Sotnikova et al., 1997). It is thought that the increased competition with the arrival of C. crocuta in Eurasia drove the extinction of P. brevirostris (Kurtén, 1988). Both H. hyaena and C. crocuta are common in Africa, the latter is also well-known from Eurasia (Guérin et al., 1993; Tchernov et al., 1994; Stiner et al., 1996; Tchernov and Tsoukala, 1997). Hyaena hyaena appears to have dispersed from Africa during the terminal middle Pleistocene as suggested by remains as Skhul and Tabun level D (Marín-Arroyo, 2013). The presence of C. crocuta in eastern Saharo-Arabia is known from a well-preserved mandible specimen from Thomas loc-3 (Thomas et al., 1998) and putatively by coprolites from Ti's al Ghadah (Stimpson et al., 2016).

56

Ursidae

Ursids are best known from Eurasia, but also from Africa during the Miocene and again with the extant *Ursus* during the Pleistocene, but mostly restricted to the northern Saharo-Arabian region (Werdelin and Peigné, 2010). Both *U. bibersoni* and *U. arctos* are known from Morocco (Freeman, 1975; Geraads et al., 1986; Geraads, 2012) and the Palearctic (Sen et al., 1991; Stiner et al., 1996; Tchernov and Tsoukala, 1997; Bar-Yosef, 2003; Stiner, 2005; Marín-Arroyo, 2013). No ursid remains have been recovered from middle Pleistocene eastern Saharo-Arabia.

Felidae

Felidae originated in Asia, and was present in Arabia (Thomas et al., 1982) and Africa (Werdelin and Peigné, 2010) in the early Miocene. The extant large felids, Panthera pardus and P. leo, likely evolved in Africa and are ubiquitous throughout the middle Pleistocene. Both P. pardus and P. leo are known from the early Pleistocene in Europe and their dispersal from Africa occurred c. 1.0 Ma (Azzaroli et al., 1988; Moullé et al., 2006). Both persisted in Eurasia throughout the middle Pleistocene (Stiner et al., 1996; Tchernov and Tsoukala, 1997; Reynaud Savioz and Morel, 2005; Stiner, 2005; Gulec et al., 2009; Roberts et al., 2014). The Eurasian P. gombaszoegensis is known from Alkhalkalaki (Hemmer et al., 2001), Kudaro I (Baryshnikov, 2002) and Lakhuti-2 (Sotnikova et al., 1997) in the Palearctic and mau have dispersed into eastern Saharo-Arabia as evidenced by tentatively ascribed remains from Ti's al Ghadah, Saudi Arabia (Thomas et al., 1998; Stimpson et al., 2015). A single tentative occurrence of P. sp. cf. P. unica was reported from Locality 73, India (Dennell et al., 2005a). The extinct Homotherium appears to have disappeared from the Oriental region around the MPT (Sotnikova et al., 1997; Hemmer et al., 2001), but is thought to have persisted in the Palearctic well into the late Pleistocene (Reumer et al., 2003). A single occurrence of the extinct *Megantereon cultridens* was reported from Locality 674 in India (Dennell et al., 2006). The presence of *Lynx thomasi* in Morocco is likely a Eurasian migrant (Geraads, 2002). Small felids are abundant during the middle Pleistocene, particularly so in East Africa, represented by *Felis* and *Caracal*.

Canidae

During the middle Pleistocene, *Canis* is the most abundant member of Canidae. In East Africa, Lainyamok has a particularly rich canid record, represented by four species and three genera (Canis, Lycaon, and Otocyon) (Potts and Deino, 1995; Faith et al., 2012). The eastern Afrotropical region is distinguished by the lack of *Vulpes*, which is common in all other regions. *Canis aureus* appears to be the most widespread canid and is known from Asbole in Ethiopia (Geraads et al., 2004), Doukkala II, Jebel Irhoud, and Aïn Bahya in Morocco (Michel and Wengler, 1993; Amani and Geraads, 1998; Geraads, 2012), Gesher Benot Ya'agov in Israel (Rabinovich and Biton, 2011), and Dursunlu in Turkey (Gulec et al., 2009). In eastern Saharo-Arabia, numerous canid cranial and post-cranial remains were uncovered from Ti's al Ghadah, the majority of which can be assigned to a medium-sized *Canis* (Stimpson et al., 2016). A single lower right M_1 can be assigned to C. anthus (Stimpson et al., 2016); a species that until recently was thought to be a subspecies of C. aureus (Koepfli et al., 2015). Small carnivore remains reported by Thomas et al. (1998) and Stimpson et al. (2015, 2016) likely represent a species of Vulpes.

Mustelidae

Mustelidae arose in Eurasia during the Late Oligocene and its dispersal into Africa occurred in successive waves that started during the Miocene (Koepfli et al., 2008), and are also known from Arabia during this time (Thomas et al., 1982; Bibi et al., 2013). Despite this, the middle Pleistocene mustelid record remains scant. Remains of *Mellivora* have been identified in the Saharo-Arabian and Afrotropical regions of Africa (Potts and Deino, 1995; Geraads, 2002; Geraads et al., 2004; Faith et al., 2012) and tentatively at 'Ubeidiya, Israel (Belmaker, 2010). *Vormela peregusna* and *Martes foina* have been identified from the Levant (Stiner, 2005; Rabinovich and Biton, 2011). A particularly diverse mustelid assemblage is noted from middle Pleistocene Georgia and included *Mustela nivalis, Meles meles, Ma foina*, and *V. peregusna* (Hemmer et al., 2001; Baryshnikov, 2002). In Saudi Arabia, a single left mandibular canine belonging to a mustelid was found at Ti's al Ghadah; its size suggesting that it may represent either a species of *Mellivora* or *Vormela* (Stimpson et al., 2016).

LATE PLEISTOCENE DISTRIBUTION

Suidae

The late Pleistocene suid record is less diverse and abundant than the preceding middle Pleistocene and except for the remains of *Kolpocerous majus* from Rusinga Island (Faith, 2014), consists entirely of extant species. During the late Pleistocene *Phacochoerus aethiopicus* is known mostly from the eastern Afrotropical region (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Assefa, 2006), as well as from Bir Tirfawi, Egypt (Gautier, 1993), and Aduma (Yellen et al., 2005), which sits roughly at the border of the Afrotropical and Saharo-Arabian realms. Today, a subspecies of *Ph.*

aethiopicus is found in the arid regions of South Africa, suggesting its distribution was previously much wider (Kingdon, 1997). This is further supported by the presence of *Phacochoerus* sp. in the Levant during the late Pleistocene (Bate, 1937). *Sus scrofa* dominates the Palearctic and Oriental regions and is also known from El Harhoura 2 Cave, Morocco (Michel et al., 2009). In the eastern Saharo-Arbian region, Delagnes et al. (2012) reported nine suid teeth and tooth fragments from western Yemen, and *Sus* remains were also reported from Jordan (Martin et al., 2010) and Iran (Trinkaus et al., 2008; Bazgir et al., 2017).

Hippopotamidae

During the late Pleistocene *Hippopotamus amphibus*, the only surviving member of the genus, is known from all regions considered here except the Oriental. The last H. amphibius populations to inhabit the Palearctic probably did so c. 50 ka, with late occurrences noted from Shanidar Cave (Evins, 1982), although, the associated layers of this site may be older than this. Hippopotamus amphibius populations persisted in the Levant along rivers that fed into the Mediterranean sea well into the Holocene (Horwitz and Tchernov, 1990). In Arabia, an indeterminate species of Hippopotamus was reported from the Empty Quater (McClure, 1984), and there is a tentatively assigned cf. *Hexaprotodon* sp. from Khall Amayshan-1 (Thomas loc-1; Thomas et al., 1998). In India, remains of Hex. ("Hip.") palaeindicus are known from numerous river valleys (Badam, 1979; 2013; Joshi et al., 1982; Chauhan, 2008). Hexaprotodon namadicus remains were reported from the Central Narmada and Godavari Valleys (Badam, 1979; Badam and Ganjoo, 1986) and Hex. sivalensis was reported from Bhagalupur, India (Verma et al., 1998). In contrast to Verma and colleagues (1998), Nanda (2008) assigned a late Pleistocene age to the Bhagalupur assemblage based

on the presence of apparently geologically young taxa (e.g. *Palaeoloxodon* sp. and *Boselapahus tragocamelus*); thus, the remains of *Hex. sivalensis* at this site are unexpectedly young and reservations are held regarding its assignment.

Camelidae

Like the middle Pleistocene, the late Pleistocene camelid record is scarce. Gautier (1966 and references therein) reported numerous *Camelus thomasi* remains from the African Saharo-Arabian regions, although Harris et al. (2010) questioned the taxonomic assignment of most specimens as they were not morphologically compared to the *C. thomasi* holotype from Tighenif. Numerous unidentified *Camelus* sp. remains are known from the Egyptian Sahara (Gautier, 1993) and the Levant (Gilead and Grigson, 1984; Griggo, 2004). *Camelus dromedarius* has been found at El Geuttar, Tunisia (Vaufrey, 1955 in Aouadi-Abdeljaouad & Belhouchet 2012). *Camelus* is know from only Umm el Tlel in Syria (Griggo, 2004) in the eastern Saharo-Arabian, but noteworthy are wild camel remains from early Holocene sites in eastern Arabia (see Uerpmann 1987).

Bovidae

Hippotraginae

Hippotragines were present during the late Pleistocene in the eastern Afrotropical region, as represented by remains of *Hippotragus equinus* (Mehlman, 1979; 1987), *Oyrx gazella* (Marean and Gifford-Gonzalez, 1991; Marean, 1992), and an unidentified species of *Oryx* (Mehlman, 1979). With the exception of *Oryx* at Aduma (Yellen et al., 2005) on the border of the Afrotropical and Saharo-Arabian realms, Hippotragines are absent from African Saharo-Arabia during the late Pleistocene, but their decline in abundance can be seen from the c. 400 ka onwards. However, O. dammah is known from large expanses across the Maghreb in historic times (Kingdon, 1997), and therefore their absence from the fossil record may reflect taphonomic or preservational biases of the late Pleistocene fossil record. In Arabia, McClure (1984) reported *Oryx* remains from the Empty Quarter and it seems likely that they represent *O. leucoryx* – a species that was abundant in Arabia until recently (Uerpmann, 1987). The remains of *O. leucoryx* have been identified at Umm el Tlel, Syria (Griggo, 2004), indicating that the species once had a wider distribution than the Arabian Peninsula.

Alcelaphinae

By the late Pleistocene the eastern Afrotropical alcelaphine record was far less abundant and diverse than earlier periods. In African Saharo-Arabia, the geographic distribution of alcelaphines during the late Pleistocene is similar to that of the middle Pleistocene. In the Levant, *Alcelaphus* is far more abundant in the late Pleistocene than the middle Pleistocene, with *A. buselaphus* remains recorded at Hayonim Cave (Stiner, 2005), Geula Cave B (Monchot et al., 2012), El Wad, and Skhul (Marín-Arroyo, 2013). *Alcelaphus* was probably also present in eastern Saraho-Arabia as Thomas et al. (1998) noted that isolated lower and upper molars from Khall Amayshan-1 likely represent an alcelaphine. A possible *A. buselaphus* was also identified from tooth fragments found in the Empty Quater (McClure, 1984).

Antilopinae

The late Pleistocene Antilopinae record of Africa and the Levant closely resembles that of the middle Pleistocene. Lukenya Hill in Kenya has a particularly rich antilopine record and includes *Oreotragus oreotragus*, *Ou*. *Ourebi*, and *Madoqua kirki* (Marean and Gifford-Gonzalez, 1991; Marean, 1992), and *M. saltiana* was found at Affad-23 in Ethiopia (Osypiński et al., 2016). In the Saharo-Arabian region, *Gazella dama*, *G. Dorcas*, and perhaps *G. rufifrons* were found at Bir Tirfawi (Gautier, 1993). The Levant remains dominated by *G. gazella*, while the Oriental antilopine record, and in particular that of the Indian subcontinent, is more abundant, diverse, and highly endemic. Endemic species include *G. bennettii*, *Antelope cervicapra*, *Procapra picticaudata*, and *Saiga tatrica* (Salim, 1986; Prasad, 1996). In eastern Saharo-Arabia, *Gazella* was identified from teeth and horn core remains recovered from the Empty Quarter and likely represents the extant and endemic *G. arabica* (McClure, 1984). *Gazella gazella* and *G. subgutturosa* are known from Karaneh IV in Jordan (Martin et al., 2010) and Umm el Tlel in Syria (Griggo, 2004), respectively.

Reduncinae

The late Pleistocene eastern Afrotropical reduncine record is similar to the middle Pleistocene with Kobus ellipsiprymnus and Redunca redunca reported from Mumba Shelter (Mehlman, 1979) and the latter from Affad-23 (Osypiński et al., 2016). Both species were also reported at Aduma (Ardu B; Yellen et al., 2005). Redunca fulvorufula, a species known from the middle Pleistocene in South Africa, is first noted during the terminal Pleistocene in Kenya (Marean and Gifford-Gonzalez, 1991; Marean, 1992), suggesting a northward expansions within the Afrotropical realm. Reduncines are found in the Egyptian Sahara but are not reported from the Maghreb. Interestingly, Vrba et al. (2015) in a revision of bovid material from Gopnath, India, reported a new species – Sivacobus sankaliai – marking the first Oriental record of a late Pleistocene reduncine. While the non-African reduncine record remains scarce, Vrba et al. (2015) suggested that members persisted in Asia following a dispersal from Africa c. 3.5 Ma, up until the late Pleistocene. Notwithstanding this, reduncines are not found in the eastern Saharo-Arabian region during the late Pleistocene.

Tragelaphinae

The late Pleistocene eastern Afrotropical Tragelaphines record resembles the middle Pleistocene. Mumba Shelter in Tanzania (Mehlman, 1979) and Porc Epic in Ethiopia (Assefa, 2006) have particularly rich tragelaphine records with remains of *Taurotragus oryx*, *Tragelaphus scriptus*, *Tr. Strepsiceros*, and possibly *Tr. imberis*. In the Saharo-Arabian region, *Tr. strepsciceros* was found at Sodmein Cave (Moeyersons et al., 2002) and Bir Tirfawi (Gautier, 1993), and an unidentified tragelaphine is reported from Haua Fteah (Klein and Scott, 1986). Tragelaphines appear to have been restricted to Africa during the late Pleistocene

Bovinae

The late Pleistocene bovine record is dominated by *Bos primigenius*. It is especially abundant in the Levant where it is has been recovered from a range of sites including Skhul (Marín-Arroyo, 2013) and 'Ein Qashish (Been et al., 2017). The rise of *Bos primigenius* appears to be correlated with a decline in *P. antiquus* abundance, which became locally extinct in East Africa during the terminal Pleistocene (Marean and Gifford-Gonzalez, 1991; Marean, 1992) but persisted in northern Saharo-Arabia into the Holocene, as evidenced by faunal remains and rock art depictions (Klein and Scott, 1986; Gentry, 2010a). The Oriental bovine record is far more diverse and abundant during the late Pleistocene. The Indian subspecies *B. (primigenius) namadicus* is known from numerous river valleys in India, including Narmada, Manjra, Krishna, and Ghod (see Chauhan, 2008 and references therein). The South Asian endemic *Boselaphus tragocamelus* was reported from Bhagalpur (Verma et al., 1998), Chintamani Gavi, and Billasurgam Caves (Prasad, 1996), and the Baghor Formation in the Son Valley (Badam, 2002 in Chauhan, 2008). Remains of *Tetracerus quadricornis* were also identified in the Son Valley (Badam, 2002 in Chauhan, 2008) and unidentified remains of *Tetracerus* sp. were found at Charnel House Cave (Roberts et al., 2014). Remains of *Bos primigenius* are known from numerous sites in eastern Saharo-Arabia (Griggo, 2004; Trinkaus et al., 2008; Martin et al., 2010), and McClure (1984) reported remains of *Bubalus* sp. and *Bos* sp. cf. *B. primigenius* from Empty Quater in Saudi Arabia.

Caprinae

Caprines were highly diverse and abundant during the late Pleistocene. The North African endemic *Ammotragus lervia* is reported from Sodmein Cave (Moeyersons et al., 2002), Haua Fteah (Klein and Scott, 1986), Rhafas Cave (Doerschner et al., 2016), and El Guettar (Vaufrey, 1955 in Aouadi-Abdeljaouad & Belhouchet 2012). *Capra aegagrus* dominates the Levantine record and *C. ibex* is known from Abu Noshra II (Phillips, 1988) and Nahal Aqev (Rabinovich, 2003). In the Oriental region, both *C. aegagrus* and *Ovis ammon* are ubiquitous. Sanghao Cave in Pakistan has an extremely rich and endemic assemblage and includes *Naemorhedus goral, Capricornis sumatraensis, Hemitragus jemlabicus*, and *Pseudois nayaur* (Salim, 1986). In eastern Saharo-Arabia, tentatively assigned remains of the Arabian endemic *Arabitragus jayakari* were found in the Empty Quarter, Saudi Arabia, as well as additional cranial and post-cranial remains attributable to either *Capra* or *Ovis* (McClure, 1984). Remains of *Ovis* spp. were reported from Wezmeh Cave and Qalehjough (Trinkaus et al., 2008; Hashemi et al., 2016) and *Capra* sp. cf. *C. aegagrus* is known from the former as well as Kaldar Cave (Bazgir et al., 2017).

Cervidae

Cervids are mostly restricted to Eurasia, although Megaceroides algericus is known from numerous late Pleistocene and Holocene localities in Northern Africa (Fernandez et al. 2015 and references therein). The late Pleistocene Levantine record strongly resembles the middle Pleistocene with the addition of *Dama dama* (Davis, 1974; Davis et al., 1988; Been et al., 2017); however, some studies suggest that D. mesopotamica is a subspecies of D. dama (see Feldhamer et al., 1988). In India, Cervus unicolor is known from the Ghod, Son, and Manjra Valleys, the latter two valleys also reporting finds of Ce. duvauceli (Badam, 1979; 2013; Joshi et al., 1981; Blumenschine and Chattopadhyaya, 1983). Axis axis was found at Charnel House Cave (Roberts et al., 2014), Billasurgam Caves (Patnaik et al., 2008), and the Baghor Formation, Son Valley (Badam, 2002 in Chauhan, 2008). Remains of Muntiacus muntjak ("Cervus muntjac") were recovered from the Baghor Formation (Badam, 2002 in Chauhan, 2008), Billasurgam Caves (Patnaik et al., 2008), and unidentified Muntiacus ("Muntjacus") sp. from Cathedral Cave (Roberts et al., 2014). Both Ce. elaphus and Capreolus capreolus are known from eastern Saharo-Arbian in Iran (Trinkaus et al., 2008; Bazgir et al., 2017) and represent the only known cervids from this region during the late Pleistocene.

Rhinocerotidae

The African late Pleistocene rhino record is similar to that of the middle Pleistocene but appears far less abundant in the fossil record. The Eurasian *Dicerorhinus hemitoechus* and *D. kirchbergensis* are known from

both northern Saharo-Arabia (Klein and Scott, 1986; Michel et al., 2009) and the Levant (Hooijer, 1961; Griggo, 2004). *Stephanorhinus* remains were found at Qalehjough (Hashemi et al., 2016) and Wezmeh Cave in Iran (Trinkaus et al., 2008); however, the former site may date to the middle Pleistocene. Both *Rhinoceros unicornis* and *R. ("karnuliensis") sondaicus* are known from India (Joshi et al., 1982; Prasad, 1996; Chauhan, 2008; Vrba et al., 2015).

Equidae

The African equid record is mostly represented by zebras, but Klein & Scott (1986) stated that some remains from Haua Fteah may be of wild ass. El Guettar may represent a late occurrence of Equus mauritanicus (Aouadi-Abdeljaouad and Belhouchet, 2012). The Levantine equid record is the most diverse and includes E. africanus, E. caballus, E. hemionus, and E. hydruntinus (Davis, 1974; 1977; Phillips, 1988; Griggo, 2004; Stiner, 2005; Marín-Arroyo, 2013). The Indian endemic E. namadicus was found in the Upper and Central Narmada, Son, Manjra, and Ghod Valleys (Badam, 1979; 2013; Joshi et al., 1981; 1982; Blumenschine and Chattopadhyaya, 1983; Badam and Ganjoo, 1986; Chauhan, 2008). The eastern Saharo-Arabia equid record is dominated by E. hemionus and remains have been reported from Shi'bat Dihya (Delagnes et al., 2012), the Empty Quarter (McClure, 1984), Ti's al Ghadah (Stimpson et al., 2016), and Wezmeh Cave (Trinkaus et al., 2008), making it one of the most common taxa in this region. Remains of E. caballus were also found at Wezmeh Cave (Trinkaus et al., 2008) and unidentified Equus sp. remains from Khall Amayshan-1 (Thomas et al., 1998) and Qalehjough (Hashemi et al., 2016).

Proboscidea

During the late Pleistocene *Elephas iolensis* is poorly known from the fossil record and is mostly restricted to the Maghreb region. Its last appearance in the fossil record is during the latest Pleistocene (Sanders et al., 2010). Remains of Loxodonta africana are found throughout Africa and occur in the late Pleistocene and Holocene layers at Omo, Kibish Formation, Ethiopia (Assefa et al., 2008). Mammuthus is unknown from regions discussed here during the late Pleistocene, but persisted in Europe until the terminal Pleistocene (Stuart, 2005). Both E. hysundricus and Stegodon insignis were found in India in the Upper Narmada and Manjra Valleys (Joshi et al., 1981; Chauhan, 2008; Badam, 2013) and the latter at Bhagalpur (Verma et al., 1998). The extant Asian elephant, E. maximus, is known from the Ghod (Badam, 1979) and Manjra Valleys (Joshi et al., 1981). Remains of E. namadicus were found in the Central Narmada Valley (Badam and Ganjoo, 1986), while tentatively assigned remains were reported from the Dhasan River in the Ganga Plain and dated to c. 56 ka (Ghosh et al., 2016). Proboscideans have not been reported from late Pleistocene deposits of the eastern Saharo-Arabia region.

Hyaenidae

Crocuta crocuta is known from all regions during the late Pleistocene, although only from a single site in the eastern Saharo-Arabian (Trinkaus et al., 2008). *Hyaena hyaena* was less common during the late Pleistocene, but remained widespread with a continued presence in the Levant as evidenced by remains from Kebara Cave (Davis, 1977; Bar-Yosef et al., 1992) and Dederiyeh Cave (Griggo, 2004). Remains of *Hyaena* sp. were reported from Kharaneh IV, Jordan (Martin et al., 2010).

Ursidae

Ursus arctos remains are abundant along the northern coasts of Morocco and Algeria during the late Pleistocene and Holocene, although their geographical range is smaller than during earlier periods (Hamdine et al. 1998 and references therein). Ursus arctos is also present in the eastern Saharo-Arabian and Palearctic regions of the Levant (Hooijer, 1961; Griggo, 2004; Stiner, 2005; Marín-Arroyo, 2013) and is known further east at Shanidar, Iraq (Evins, 1982), and Wezmeh Cave, Iran (Trinkaus et al., 2008). The South Asian endemic, *Melursus* sp., was reported from Billasurgam Caves, India (Prasad, 1996).

Felidae

The late Pleistocene felid record consists solely of extant members. The large-bodied felid record of Africa is far scarcer during the late Pleistocene than in the preceding middle Pleistocene. Panthera pardus was found at Sodmein Cave in the Egyptian Sahara (Moeyersons et al., 2002), P. leo at Lukenya Hill in Kenya (Marean and Gifford-Gonzalez, 1991; Marean, 1992), and both at El Harhoura 2 Cave in Morocco (Michel et al., 2009), suggesting a widespread distribution. The Eurasian large felid record is perhaps more abundant during the late Pleistocene and both P. pardus and P. leo are known from numerous sites (Hooijer, 1961; Gilead, 1991; Griggo, 2004; Stiner, 2005; Otte et al., 2007; Patnaik et al., 2008; Trinkaus et al., 2008; Monchot et al., 2012), and the present-day restricted range of the latter to Africa (and a small pocketed population in India) is likely an modern anthropogenic artefact. Both large (P. pardus and P. leo) and small felids (F. silvestris) were reported from Wezmeh Cave, Iran (Trinkaus et al., 2008). Notable is the appearance of the Asian P. tigris at the Billasurgam Caves (Prasad, 1996). Small-bodied felids are common again in the Eurasia.

Canidae

Canids were found in all regions during the late Pleistocene. In terms of abundance, *Vulpes Vulpes* was most common except in the eastern Afrotropical region (although the canid record is noticeably scant). In eastern Saharo-Arabia, *Vulpes* is known from Kharaneh IV, Jordan (Martin et al., 2010), and Wezmeh Cave, Iran (Trinkaus et al., 2008). Both *Canis lupus* and *C. aureus* are known from the Palearctic region of the Levant (Hooijer, 1961; Phillips, 1988; Stiner, 2005; Monchot et al., 2012) and the latter from northern Saharo-Arabia (Michel et al., 2009).

Mustelidae

Fossil remains of mustelids were far more common during the late Pleistocene than in the preceding middle Pleistocene. *Melivora capensis* is known widely from Africa (Marean and Gifford-Gonzalez, 1991; Marean et al., 1992; Michel et al., 2009) and Guela B Cave, Israel (Monchot et al., 2012). *Meles meles* and *Martes foina* are known from numerous sites in the Levant (Hooijer, 1961; Stiner, 2005; Monchot et al., 2012; Marín-Arroyo, 2013) and the latter from Yafteh Cave in India (Otte et al., 2007). In Turkey, Wezemeh Cave has a particularly rich mustelid record with *Mustela putoris, Ma. martes, Me. meles* present (Trinkaus et al., 2008), the latter also present at Yafteh Cave in India (Otte et al., 2007).





Figure 2. (above). Temporal distribution of major bovids from the discussed regions drawing from this review and extended literature. Thick solid lines indicate securely known temporal distribution and dotted lines indicate possible chronologies, mostly from tentatively assigned remains. Solid black sections of the left axis represent periods of normal polarity, while white sections indicate periods of reversed polarity. Horizontally lying grey rectangle highlighting first-and/or last-appearance datums *c*. 400-600ka. Silhouettes of animals from http://phylopic.org by Michael Keesey, Brian Gratwicke, Oscar Sanisidro and Steven Traver.

Figure 3. (below). Temporal distribution of major non-bovid ungulates, Proboscidea and carnivores from the discussed regions drawing from this review and extended literature. Camels have been excluded owning to poor fossil record and uncertainty surrounding numerous identifications. Thick solid lines indicate securely known temporal distribution and dotted lines indicate possible chronologies, mostly from tentatively assigned remains. Solid black sections of the left axis represent periods of normal polarity, while white sections indicate periods of reversed polarity. Horizontally lying grey rectangle highlighting first- and/or last-appearance datums *c*. 400-600ka. Silhouettes of animals from http://phylopic. org by Jan A. Venter, Herbert, H. T. Prins, David A. Balfour, Rob Slowtow, Michael Keesey, Rebecca Groom and Steven Traver.





DISCUSSION

Considerable shifts in African and Eurasian faunal assemblages, attributable to changes in climate throughout the Plio-Pleistocene, have long been recognised (Azzaroli, 1983; Vrba, 1985; 1992; 1993; Azzaroli et al., 1988; Bobe and Behrensmeyer, 2004). Vrba (1985; 1992; 1993) proposed the Turnover Pulse hypothesis to explain apparent 'pulses' of extinction and speciation (i.e. discrete punctuated periods of rapid extinction and speciation) that may have coincided with significant shifts in climate. Specifically, Vrba noted significant and rapid increases in the diversity and abundance of aridadapted ungulates (i.e. alcelaphines and antelopines) coeval with cooling and aridification during the Plio-Pleistocene. Conversely, others have suggested more continual and gradual change took place at those times (e.g. Behrensmeyer et al., 1997; Bibi and Kiessling, 2015). Potts (1998) documented a reversal in the trend toward highly-specialised taxa c. 1.0 Ma at Olorgesailie and proposed that increased climatic variation would drive selection in favour of more versatile, or generalist, taxa ("Variability Selection" hypothesis). Furthermore, Potts and Faith (2015) found hominin technological innovation events corresponded with environmental variability. The timing and nature of the apparent widespread faunal turnovers identified here can be viewed in light of environmental fluctuations. Below we discuss the biogeographical trends and turnovers in context with the eastern Saharo-Arabian faunal record and the implications for hominin dispersal into Arabia.

Biogeographical trends and turnovers

Faunal evidence indicates that there was little exchange between Africa and Eurasia between c. 1.2–0.78 Ma (O'Regan et al., 2005; Belmaker,

2009; Geraads, 2010a; 2012). Large-bodied carnivores are an exception, as evidenced by the appearance of African taxa (e.g. *Panthera pardus* and *Crocuta crocuta*) in Europe during the late early Pleistocene (c. 1.0–0.9 Ma) (Azzaroli, 1983; Azzaroli et al., 1988; Moullé et al., 2006). The extinction of the large *Pachycrocuta brevirostris* occurred c. 0.9–1.0 Ma in Eurasia, potentially as a result of increased competition with C. crocuta (Kurtén, 1988). Possible occurrences of African taxa are noted at 'Ubeidiya in the Levant (*Pelorovis oldowayensis*, *Giraffa* sp.), however, the assemblage is mostly Eurasian and this connection should not be overstated (Geraads, 2010a). Belmaker (2009) recognised a minor turnover event in the Levant c. 1.0 Ma with the disappearance of species such as *Praemegaceros verticornis* and *Mammuthus meridionalis* and the *in situ* speciation of *Kolpochoerus evronensis*. The lack of new migrant species during this event reiterates the ecological separation between Africa and Eurasia during this time and this continues into the middle Pleistocene.

The MPT is characterised by periods of marked aridity, grassland expansion, and overall heightened climatic variability, triggered by the 41 kyr to 100 kyr shift in glacial cycles (deMenocal, 2004). Associated with the amplified climate variability is a shift from large-bodied, highly hypsodont, arid-adapted fauna toward smaller-bodied taxa with flexible diets (Potts, 1998; Faith et al., 2012; Faith, 2014). Our review suggests that the most significant change in middle and late Pleistocene African and Eurasian faunal assemblages occurred following the MPT, and more specifically between 400–600 ka (Fig. 2 and 3). Most notable is the replacement of arid-grassland adapted suids (*Metridochoerus* spp., *Kolpochoerus* spp.), alcelaphines (*Megalotragus kattwinkelli*, *Damaliscus niro*), and the highly amphibious hippos (*Hippopotamus gorgops*, *H. behemoth*) by closely related generalists (Figs. 2 and 3). The hypsodont hipparione horses, large-bodied Equus oldowayensis, and Palaeoloxodon recki also disappeared during this period, the latter corresponding with the rise in abundance of the extant mixed-feeder/browser Loxodonta africana (Sanders and Asmussen, 2010). Klein (1988) also suggested that the disappearance of *P. recki* from the South African fossil record resulted from the MPT shift in glacial cycles and increased competition with ungulates. Other notable African extinctions that followed the MPT but prior to the 400–600 ka event include *Hippotragus gigas*, *Parmularius spp.*, and *Antidorcas recki*, all species known to be specialised grazers (Stynder, 2009). Contrary to this trend, arid-adapted wild asses (*E. hemionus* and *E. hydruntinus*) appear in the eastern Saharo-Arabian and Oriental regions and dominate the equid record during this period.

Despite increased aridity in the Sahara, the mixed feeder/browser Taurotragus oryx (Stynder, 2009), as well as Alcelaphus buselaphus, appeared in the Afrotropical and Saharo-Arabian c. 400–600 ka, suggesting a continued connection between these two regions. Such dispersals may have been facilitated by the establishment of palaeohydrological corridors in the Sahara during interglacials (Drake et al., 2011; Scerri et al., 2014a). Three Eurasian migrants, Sus, Cervus and Stephanorhinus, are first reported in Morocco during this time, indicating a strengthening Eurasian influence in the African Saharo-Arabian regions (although the identification of this material has been questioned, Geraads, 2012). Potts and Deino (1995) and Faith et al. (2012) interpreted the arrival of an almost fully extant and more 'versatile' faunal assemblage at Lainyamok in the eastern Afrotropical region as a significant faunal turnover occurring c. 400–500 ka. Furthermore, at c. 430 ka, Belmaker (2009) identified a minor turnover in the Levant with the extinction of species of the large-bodied Megaloceros, Ovibovini, and Pelorovis. Regardless, extant cervids and suids dominate the Levantine

faunal record relatively early, suggesting more stable conditions and/or versatile taxa than in contemporary Africa.

Palaearctic component in northwest Africa continued to The strengthen during the late middle to early late Pleistocene with the aridification of North Africa and extirpation of Afrotropical ungulates (e.g. Hippotragus, Taurotragus oryx, and reducines). Stiner et al. (2004 in Belmaker, 2009) attributed increased Gazella abundance in the Levant during the late Pleistocene to climate change, and this taxon is particularly prevalent at sites such as Ohalo II (Rabinovich, 2003) and El Wad D (Marín-Arroyo, 2013). On the basis of the information discussed here, Alcelaphus is also more abundant during the late Pleistocene than during the middle Pleistocene and likely represented an established population. In addition, caprines became more diverse and abundant during the late Pleistocene in the Palearctic and Oriental regions and wild asses dominate the equid record. During this period, few, if any, African bovids migrated into the Eurasia. Alcelaphus buselaphus may represent an African migrant, but a continual presence since the middle Pleistocene is equally possible and may have been a stable part of the Palearctic and eastern Saharo-Arabian faunal communities. The presence of Struthio and Camelus at Qafzeh has been argued to indicate northward expansion of African savanna into the Levant (Tchernov, 1992). However, given the overall Eurasian nature of this site, Struthio remains from India during the late Pleistocene (Blinkhorn et al., 2015; Jain et al., 2017), and the poor Camelus fossil record, suggest that this claim is overstated. In Africa, selection toward generalist mixed-feeders continues throughout the late Pleistocene and into the Holocene (e.g. increased abundance in *Taurotragus oryx and Tragelaphus* spp.) and is suggestive of continual reduction in open grasslands (Faith and Behrensmeyer, 2013; Faith, 2014). For example, Faith, (2014) noted that ~15
species of Alcelaphini went extinct over the last one million years, many of which occurred during the late Pleistocene. Contrary to this, very little extinction has taken place on the Indian subcontinent over the last 200 kyr, suggesting that fauna from this region were little affected by the environmental change or that climate change was less dramatic than in contemporary Africa (Roberts et al., 2014). We suspect that the apparent appearance of many new species, namely that of caprines and antilopines, identified in Pakistan (Salim, 1986), is a result of the patchy fossil record and/or taphonomic bias of this region and not a true turnover in fauna.

African and Eurasian connections in Arabia

Arabia sits at the geographic crossroads of Africa and Eurasia and this is clearly reflected in its fossil record. During the middle and late Pleistocene, Arabia experienced influxes of African, Palearctic, and Oriental large mammals, and was also home to some endemics (A. jayakari and G. arabica). The Arabian endemics have likely had a long-term presence in Arabia, as supported by phylogenetic studies suggesting species divergence prior to the Pleistocene (Ropiquet and Hassanin, 2005; Lerp et al., 2013). Stimpson et al. (2016) suggested that Oryx remains from the western Nefud Desert may represent the ancestral progenitor of the Arabian endemic O. leucoryx, and their presence in Arabia likely pre-dates the Pleistocene. The majority of taxa identified in the Arabian fossil record had wide geographic distributions during the middle and late Pleistocene, and some species (e.g. C. crocuta) are found in all regions discussed here. This makes it difficult, if not impossible, to determine the origins of many Arabian taxa on the basis of fossil evidence alone. Nonetheless, regional influences are clear. Interestingly, a Eurasian influence is perhaps stronger than previously thought (Thomas et al., 1998). In terms of the number of occurrences, the Asiatic wild ass, E. hemionus, is

one of the most common species found during the middle and late Pleistocene. Extant wild asses tend to inhabit arid landscapes and can subsist on poor-quality forage (Faith, 2014), and were common throughout the Levant well into the Holocene (Uerpmann, 1987). It seems possible that *E. hemionus* persisted in eastern Saharo-Arabia, or repeatedly dispersed from the North, during climatic amelioration. The presence of both *Bubalus* and *Capra* suggest a Eurasian influence during the late Pleistocene; however, the former identification should be considered tentative as remains were not described in detail (McClure, 1984). Nonetheless, their dispersal from the Palearctic into southern Arabia seems plausible. The tentative presence of the large Eurasian endemic *P. gombaszogensis* at Ti's al Ghadah would represent the southernmost extent and a late occurrence of this species (Stimpson et al., 2016), and is the best example of a Eurasian influence in Arabia. Furthermore, its presence suggests a substantial vertebrate prey biomass in the region (Stimpson et al., 2016).

An African influence in Arabia is perhaps best represented by the occurrence of *Pelorovis* during the middle and late Pleistocene. *Pelorovis* was widespread during the middle Pleistocene, but by the late Pleistocene it was mostly restricted to the Maghreb and Egypt, and its presence in the eastern Saharo-Arabian region at Khall Amayshan-1 likely represents an eastward dispersal from North Africa. Alcelaphini are mostly restricted to Africa during the middle Pleistocene and their presence in Arabia is suggestive of an African connection. During the late Pleistocene, however, *Alcelaphus buselaphus* appears established in the Palearctic region of the Levant and thus the connection with the Arabian late Pleistocene alcelaphini is more ambiguous. Alcelaphines (Kingdon, 1997), and likely *Pelorovis* (Bibi, 2007), are obligate drinkers and their presence in Arabia probably represent repeated dispersal events, as these taxa are unlikely to survive under very

arid conditions. They may have persisted elsewhere on the Arabian Peninsula during arid phases, perhaps making use of highland refugia (e.g. Yemeni highlands or Hajar Mountains), regions which are known to host less arid-adapted taxa today (Parker and Rose, 2008). Recent genetic work by Koepfli et al., (2015) also identified *Canis anthus* as an African species distinct from *C. aureus*, and thus represents a carnivoran biogeographical connection between Africa and Arabia

Implications for hominin dispersals into Arabia

Owing to a wealth of archaeological research in recent years, it appears that hominins inhabited the Arabian Peninsula by the middle Pleistocene (e.g. Groucutt and Petraglia, 2012; Rosenberg et al., 2013; Shipton et al., 2014; Scerri et al., 2015; Bretzke et al., 2017). The chronology of Acheulean sites in Arabia is currently unclear. Of interest in the current debate is the recovery of a low-density surface lithic assemblage at Ti's al Ghadah (Scerri et al., 2015). This has broad similarities with assemblages from the Levant assigned to the Yabrudian, although this similarity should not be overstated. The Ti's al Ghadah lithics may relate to stratified deposits at the site dated to c. 318–554 ka (Rosenberg et al., 2013; Stimpson et al., 2016). Hominins dispersing southwards from the Levant would have encountered a similar taxonomic composition in Arabia, including both prey (Oryx, Equus hemionus and Alcelaphini) and predator/competitor species (Crocuta crocuta). Possible novel taxa for hominins migrating south from the Levant are C. anthus and *Pelorovis.* Middle Pleistocene sites from the western Nefud Desert are roughly contemporaneous with interglacial periods and it seems reasonable to suggest that dispersal of fauna in the Arabian interior, with the exception of arid-adapted species (e.g. Oryx), occurred during these periods of climatic amelioration. Panthera sp. cf. P. gombaszogensis and E. hemionus were likely

80

novel taxa to hominins dispersing from Africa during the middle Pleistocene, but overall, the taxonomic composition of middle Pleistocene Arabia would have been similar to that of East African grasslands and the behaviours of these animals are likely to closely mimic related taxa in Africa. Regardless of origin, the grassland habitat and taxonomic similarities between Arabia on the one hand, and the Levant and Africa on the other, suggests that expansion into Arabia did not require significant behavioural and/or technological innovation for migrating hominins.

During the late Pleistocene, hominins inhabited a wide geographical range in Arabia, stretching from the western Nefud Desert and across to the coasts of Oman and Yemen (Groucutt and Petraglia, 2012). Unfortunately, the faunal record for this period is much poorer than for the middle Pleistocene. It seems likely that the appearance of *Capra* and *Bubalus* in the Empty Quarter represent dispersals from highlands refugia, and hominin movement into the interior may have followed such taxa. It seems reasonable to suggest that hominins migrated into the western Nefud Desert from northeast Africa following dispersing ungulates, which is also consistent with similarities in lithic assemblages between the two areas (Scerri et al., 2014b). Although the fossil record remains patchy, future exploration and research will undoubtedly result in better informed hypotheses regarding hominin dispersals into the region

CONCLUSIONS

This review agrees with previous studies that identified the replacement of large-bodied specialists with more versatile taxa in response to heightened climatic variability over the past million years. The most significant turnover occurred c. 400–600 ka in Africa, with similar, albeit

dampened, shifts in Levantine faunal assemblages during this period. It's likely that climatic amelioration over the Arabian Peninsula, coupled with significant turnover in the surrounding regions, drove the dispersal of fauna (including hominins) into Arabia from both Africa and Eurasia. Subsequent environmental deterioration likely resulted in fauna retreats, extirpations, and possibly speciation. Some species may have made use of highland refugia when poor conditions dominated the interior, and only returned when suitable environments resumed. Most of the taxa identified from Arabia had widespread distributions during the Pleistocene and it is difficult to determine the origin of these taxa on fossil evidence alone. Regardless, distinctly Eurasian and African taxa were present in Arabia during the Pleistocene, and it is clear that the Arabian faunal record represents a composite of both regions. Hominins dispersing into Arabia from Africa (via the far south of the Levant), the northern Levant, or the Bab el-Mandeb Strait would have encountered familiar taxa and open-grassland habitats. These comparable biota and habitats suggest that hominins dispersing into Arabia did not require significant behavioural and/or technological innovation for subsistence. However, the Arabian Pleistocene fossil record is still very patchy, and our interpretation remains preliminary. Future exploration, particularly of the late Pleistocene fossil record, will allow for the framing of more precise hypotheses regarding faunal turnovers in the region and its potential implications for hominin dispersals and adaptations. Quantitative approaches for assessing similarities between Arabia and the surrounding regions are the next steps in comparative studies, especially as the Arabian fossil record grows with more exploratory surveys and excavations.

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CHAPTER THREE

Fossil herbivore stable isotopes reveal middle Pleistocene hominin palaeoenvironment in 'Green Arabia'

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Declaration

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Mathew Stewart

*The project was conceived and led by MS and PR. MS conducted the taxonomic, taphonomic, and imaging analysis of the fossil material. PR conducted the isotope analysis. Both MS and PR prepared the manuscript and all co-authors contributed to the final manuscript. MS and PR are corresponding and equally contributing authors.

ABSTRACT

Despite its largely hyper-arid and inhospitable climate today, the Arabian Peninsula is emerging as an important area for investigating Pleistocene hominin dispersals. Recently, a member of our own species was found in northern Arabia dating to c. 90 ka, while stone tools and fossil finds have hinted at an earlier, middle Pleistocene, hominin presence. However, there remain few direct insights into Pleistocene environments, and associated hominin adaptations, that accompanied the movement of populations into this region. Here, we apply stable carbon and oxygen isotope analysis to fossil mammal tooth enamel (n=21) from the middle Pleistocene locality of Ti's al Ghadah in Saudi Arabia associated with newly discovered lithics and probable cutmarks. The results demonstrate productive grasslands in the interior of the Arabian Peninsula c. 500–300 ka, as well as aridity levels similar to those found in open savanna settings in eastern Africa today. The association between this palaeoenvironmental information and the earliest traces for hominin activity in this part of the world lead us to argue that middle Pleistocene hominin dispersal into the interior of the Arabian Peninsula required no major novel adaptation.

INTRODUCTION

Studies of Pleistocene hominin dispersals beyond Africa are important for understanding the course of global human evolution and prehistory. In particular, analysis of the environmental context under which members of the genus Homo moved into Europe and Asia in the early and middle Pleistocene (2.6 Ma to 126 ka) relative to that of *Homo sapiens* populations expanding around the globe in the late Pleistocene (126-12 ka) can provide insight into the potential ecologically unique nature of our species (Gamble, 1993, 2013; Roberts and Stewart, 2018). It has recently been highlighted that our species occupied and utilized a diversity of extreme environments, including deserts, tropical rainforests, Palaearctic, and high-altitude settings around the world during the late Pleistocene (Roberts and Stewart, 2018). By contrast, the dispersals of earlier Homo species into Europe and Asia appear to be best associated with generalized utilization of different forest and grassland mosaics proximate to riverine and lacustrine settings (Gamble, 1993, 2013; Dennell and Roebroeks, 2005). However, a paucity of associated palaeoenvironmental information has made it difficult to systematically test this distinction and many hold that non-H. sapiens members of the genus Homo demonstrate significant cultural (Joordens et al., 2016; Hoffman et al., 2018) and ecological (Morwood et al., 1998; Zhu et al., 2008; Parfitt et al., 2010) flexibility.

In spite of its crucial geographic position at the interface of Africa and Eurasia, the Arabian Peninsula has remained remarkably absent from models of Pleistocene hominin expansions until relatively recently, owing to a lack of well-constrained archaeological and palaeoecological data. Climate modelling (Jennings et al., 2015), speleothem records (Fleitmann et al., 2003), palaeontological findings (Thomas et al., 1998; Stimpson et al., 2015, 2016; Groucutt et al., 2018), and geomorphological studies of palaeolake records (Rosenberg et al., 2013; Parton et al., 2015) have been used to argue that at intervals in the past, notably during interglacials, the harsh, hyper-arid deserts that cover much of Arabia today were replaced by 'moister' and 'greener' conditions more hospitable to foraging occupation (Groucutt et al., 2015; Breeze et al., 2016). Furthermore, the find of a H. sapiens phalanx, in association with Middle Palaeolithic stone tools, at the site of Al Wusta dated to c. 90 ka provides definitive evidence for the early presence of our species in the interior of the Arabian Peninsula (Groucutt et al., 2018). There have also been suggestions that finds of stone tools in the Arabian interior are associated with an earlier period of middle Pleistocene hominin dispersal (Armitage et al., 2011; Petraglia et al., 2011; Scerri et al., 2015). However, despite the significance of climate and environmental change for hominin dispersal into the region, there has been no direct means of determining what 'wetter' represents in the context of regional ecology, nor definitive identification of middle Pleistocene hominin presence.

We undertook renewed archaeological and taphonomic analysis of fossil fauna found at the middle Pleistocene (c. 500–300 ka) fossil locality of Ti's al Ghadah in the Nefud Desert of Saudi Arabia (Fig. 1 and 2). Ti's al Ghadah is one of the most important palaeontological sites in the region, representing the largest and best-preserved faunal assemblage recovered from Pleistocene Arabia (Thomas et al., 1998; Stimpson et al., 2015, 2016). Previous analyses have identified a suite of terrestrial and aquatic animals, including extinct elephants (*Palaeoloxodon* sp.), horses (*Equus hemionus*), and water birds (*Tachybaptus* sp. and *Anas* sp.) that have been used to argue the western Nefud Desert was significantly less arid at times during the middle Pleistocene than it is today (Thomas et al., 1998; Stimpson et al., 2015, 2016). 'Middle Palaeolithic' artefacts of unknown age have also been
recovered from the surface of the basin (Scerri et al., 2015). Yet, the lack of taphonomic analysis and scarcity of anthropogenic remains has made evaluating the relationship between hominins and fossil fauna difficult. Furthermore, there has also been no way of analysing, in detail, the vegetation and relative aridity associated with the middle Pleistocene Ti's al Ghadah fossil assemblage. To remedy this, we performed stable carbon (δ^{13} C) and oxygen (δ^{18} O) isotope analysis of 21 fossil fauna recovered from Ti's al Ghadah. All fossils were recovered from a discrete unit (Unit 5) with little evidence of reworking or redeposition (Stimpson et al., 2016), suggesting that time-averaging was probably minimal (see also *Chapter Four*). δ^{13} C can provide detailed insight into the different types of biomass in animal diets (Lee-Thorp et al., 1989a, 1989b; Levin et al., 2008), whereas δ^{18} O can be used to investigate humidity and precipitation (Levin et al., 2006; Blumenthal et al., 2017).

A variety of tissue types have been used to investigate animal diets. Bone collagen and bone apatite provide the longest, averaged signature of diet due to the continuous turnover of these bone tissue throughout the life an individual (Hedges et al., 2007). However, collagen is susceptible to rapid degradation, particularly in hot and humid climates (Krigbaum, 2001, 2003), whereas apatite is vulnerable to chemical alteration (Lee-Thorp, 2008). The efficacy of these tissue types in archaeological and/or palaeontological studies is therefore compromised. Tooth enamel, on the other hand, comprises a hydroxyapatite crystal lattice that is more resistant to diagenesis than other tissue types (Lee-Thorp et al., 1989a; Wang and Cerling, 1994; Lee-Thorp, 2000, 2008). The preserved carbonate structure provides an accurate measure of the bulk diet of an individual (Ambrose and Norr, 1993; Lee-Thorp et al., 1989a), making tooth enamel the preferred bone tissue in stable isotope studies across a variety of environments (e.g. Krigbaum, 2001, 2003, 2005; Lee-Thorp, 2008; Ecker et al., 2013; Roberts et al., 2017). Finally, since tooth enamel forms incrementally, sequential δ^{13} C and δ^{18} O analysis be used to look at temporal changes in vegetation and water source during the period of tooth enamel formation (Balasse, 2002).



Figure 1. Maps showing A) the position of the Ti's al Ghadah fossil site and the Mahazat as-Sayd Protected Area in the context of Saudi Arabia and B) A view of the Ti's al Ghadah basin showing in blue the extent of the lacustrine deposit overlying the main fossil faunal deposit.

STABLE CARBON ISOTOPE ANALYSIS

The primary driver of δ^{13} C variation in the majority of terrestrial ecosystems, including within the Arabian Peninsula, is the marked isotopic distinction between the two dominant terrestrial photosynthetic pathways, C₃ and C₄, which differ in their net discrimination against ¹³C during the fixation of CO₂ (Craig, 1953; Smith, 1971; Farquhar et al., 1989). Plants making use of the C₃ pathway, including most trees, woody shrubs, herbs, and temperate or shade-loving grasses, have highly negative δ^{13} C (about -24 to -36‰; global mean = -26.5‰) as a result of strong discrimination against ¹³C. Plants using the C₄ photosynthetic pathway, typically tropical grasses 115 (about -9 to -17‰; global mean = -12‰), which make more efficient use of available CO₂, do not discriminate as strongly against the heavy ¹³C isotope. C₃ and C₄ δ^{13} C is therefore distinct and non-overlapping. This picture is made more complex by Crassulacean Acid Metabolism (CAM) plants that can have overlapping δ^{13} C values to C₃ or C₄ plants, and often exist in arid regions, though these plants tend to be rare relative to other plant types and are not usually dominant in mammalian herbivore diets (O'Leary, 1981).

These photosynthetic pathways are adaptive responses to prevailing environmental conditions (Tieszen et al., 1991). The strongest determinant for C_4 plant distribution is growing season temperature (Ehleringer et al., 1997; Vogel et al., 1978). Few C_4 species thrive at minimum growth-season temperatures below 8°C, while Vogel et al. (1978) recorded the crossover maximum summer temperature for C_4 biomass domination (> 50%) in South Africa as at least 25 °C. In highland areas this results in an altitudinal transect with C₄ biomass often dominant at lower, warmer altitudes but almost completely absent from colder, high-altitude locales (Tieszen et al., 1979; Livingstone and Clayton, 1980; Smith et al., 2002). In other contexts, including Arabia, C₃ plant taxa can be found primarily within forest, woodland, or more shaded grassland ecologies, with C4 grasses and sedges being restricted to more open, insolated, warmer grassland biomes (Cerling and Harris, 1999). Variation within the C_3 photosynthetic pathway itself can also be linked to altitude, irradiance, temperature, salinity, humidity, nutrient availability, and partial pressure of atmospheric CO_2 (Smith et al., 1976; Farquhar et al., 1982; Ehleringer et al., 1986).

Studies have demonstrated that δ^{13} C measurements of faunal tooth enamel are reliable recorders of animal diet and behaviour (Lee-Thorp and van der Merwe, 1987; Cerling et al., 2003a, 2003b, 2004). In herbivores they have been shown to record the dietary proportion of C₃ closed canopy, C₃, and C_4 resources, and thus provide a robust environmental indicator of the presence and prominence of these biomes. For example, Levin et al. (2008) used modern faunal tooth enamel from Central and East Africa to track environmental variation from the closed-canopy C_3 habitats of the Ituri Forest, Democratic Republic of Congo (-26.0 to -14.1‰), to the open C_3/C_4 grasslands of East Africa (-12.0 to 0.2‰). In pre-fossil fuel herbivore diets tooth enamel with $\delta^{13}C$ of *c*. -12‰ indicates a diet 100% dominated by C_3 vegetation while $\delta^{13}C$ of *c*. 0‰ is indicative of a diet 100% dominated by C_4 vegetation (Lee-Thorp et al., 1989a, 1989b; Levin et al., 2008). Relative contributions of CAM plants are more difficult to predict in this way, however.

The exact δ^{13} C end-values for C₃ and C₄ plants are context specific. For robust comparisons of δ^{13} C measurements through time, variations in the isotopic composition of the atmosphere through time must be considered. $\delta^{13}C$ of modern atmospheric CO₂ (-8‰) is more depleted than the δ^{13} C of CO₂ in the pre-industrial atmosphere (Francey et al., 1999), with less dramatic variations evident further back into the Pliocene and Miocene (Zachos et al., 2001; Levin et al., 2008). This must be taken into account, especially when comparison is made between modern and pre-industrial datasets. shifts Furthermore, in atmospheric CO_2 concentration (p CO_2) on glacial/interglacial timescales affect the relative abundance of C_3 and C_4 species, as C₄ plants are at an advantage during conditions of lowered pCO₂ the Last Glacial Maximum), an additional complication for (e.g. environmental interpretation (Ehleringer et al., 1997). This additional factor has been shown to potentially alter the baseline δ^{13} C values of fauna between the Last Glacial Maximum and Holocene period by a maximum of c. 0.5‰ (Hare et al., 2018).

STABLE OXYGEN ISOTOPE ANALYSIS

Global patterns of $\delta^{18}O$ of precipitation are first and foremost structured by temperature dependent processes of evaporation from the oceans, the Rayleigh distillation effect during rainout as moisture masses across continents, and the amount effect (Dansgaard, 1964; Gat, 1996). Fractionation, affecting precipitation δ^{18} O from these moisture sources, is negatively influenced by temperature (latitude), rain-out, or Rayleigh distillation effects that vary with distance from the oceanic source ("continental effect"), and an "amount effect" related to heavy rain (Dansgaard, 1964; Rozanski et al., 1993). Evaporation exerts a positive effect on δ^{18} O, particularly in arid desert regions such as the centre of the Arabian Peninsula, so that continental water bodies and soils in areas with a water deficit are ¹⁸O-enriched. These factors lead to variations in both precipitation and groundwater $\delta^{18}O$ across space and time. In Pleistocene Arabia it is known that various water sources, including African westerlies, the Indian Ocean Monsoon system, and the Mediterranean westerlies, may have all variously contributed to Pleistocene precipitation and groundwater (Jennings et al., 2015).

The source water for plants is soil moisture, so part of the signal in plant δ^{18} O is a sum of the isotope effects on soil water plus evapotranspiration in leaves that leads to preferential loss of ¹⁶O and ¹⁸O enrichment in the leaf (Gonfiantini et al., 1965). The magnitude of this effect is enhanced by low relative humidity (increased aridity) (Flanagan et al., 1991; Barbour, 2007). Since the leaf is the site of photosynthesis, and photosynthate products are used to construct the non-photosynthetic plant parts such as wood, stems, and fruits, the effects of evapotranspiration are effectively disseminated through the plant (McCarrol and Loader, 2004). It is important to note that while evaporation will lead to higher δ^{18} O in open water bodies, such as lakes and 118 rivers, in arid conditions, the evaporation effects and δ^{18} O increases seen in plant water and plant tissues under the same conditions will be more acute given these additional enrichments from the groundwater (Gonfiantini et al., 1965). This is a universal principle that operates in all environmental settings around the world and will be particularly obvious in water-stressed or arid settings (Sponheimer and Lee-Thorp, 2001; Barbour, 2007).

 δ^{18} O in mammalian tooth enamel bioapatite is largely determined by the δ^{18} O of ingested water, both from drinking water and plant/food water (Luz and Kolodny, 1984; Longinelli, 1984), as well as from oxygen associated with plant carbohydrates. Given the impacts of humidity on evapotranspiration and plant water and tissue $\delta^{18}O$ noted above, tooth enamel δ^{18} O has been used as a proxy for relative humidity (Longinelli, 1984; Quade et al., 1995). However, variation in δ^{18} O by temperature and precipitation source, particularly in Arabia where sources are known to have changed in the past (Jennings et al., 2015), has limited the use of this methodology in palaeoenvironmental studies. Nevertheless, certain physiological and behavioural variables that influence how faunal enamel δ^{18} O responds to changes in water deficit or evaporative potential (Gat, 1996; Sponheimer and Lee-Thorp, 2001; Levin et al., 2006; Blumenthal et al., 2017) offer a means to circumvent this issue. Herbivores that obtain most of their water from plant sources (non-obligate drinkers) have tooth enamel δ^{18} O that not only reflects local rain, but also relative environmental humidity (the main source of fractionation in plant leaf water δ^{18} O). Obligate drinkers are not as sensitive to this environmental factor (Levin et al., 2006; Blumenthal et al., 2017). As a result, the difference in $\delta^{18}O$ between non-obligate and obligate drinker tooth enamel will provide insights into relative aridity. This will remain the case regardless of changes in precipitation source or temperature.

Levin et al. (2006) and Blumenthal et al. (2017) have studied non-obligate and obligate drinkers across a series of environments with different degrees of aridity and water deficit in East Africa. They have used this data to calculate species-specific gradients for determining the local water deficit based on the δ^{18} O of tooth enamel. However, each species-specific gradient is based on a relatively small number of samples and its use is contingent on analysing the same species in the present as the past. As a result, we do not use any of their equations to calculate an 'aridity index'. Instead, in this paper, we seek to use the basic principle of obligate and non-obligate drinkers to compare aridity in modern central Saudi Arabia, East African open 'savanna' settings, and middle Pleistocene Ti's al Ghadah on a relative basis. This comparison does not provide absolute numbers for water stress, humidity, or potential evapotranspiration. Rather, it enables a relative comparison of these different environments, allowing a rough approximation of the environmental stresses placed on animals in Pleistocene 'Green Arabia'.

SITE BACKGROUND

The site of TAG is situated within an interdunal basin in the southwestern Nefud Desert, approximately 95 km southeast of the city of Tayma, Saudi Arabia. The basin is flanked on both sides by megabarchan dune ridges, while smaller linear dunes form its northern and southern edges. In the centre of the basin is a 630 m long palaeolake deposit that rises markedly above the modern basin floor and orientated NW-SE. The deposit is comprised of interdigitated units of lacustrine marls, surficial sheetwash, and aeolian sands that have been interpreted as multiple phases of environmental wetting and drying (Fig. 2) (see Stimpson et al., 2015, 2016 and *Chapter Four* for detailed description of entire sequence). This study is

concerned with the youngest deposits at the site which cap this sequence and contain the greatest abundance in fossil remains (Units 5–9; Fig. 2). Unit 5 is the oldest deposit discussed here and consists of weakly cross-bedded coarse green sands with occasional quartz pebbles and iron-stained root casts. Units 6–8 consist of diatomaceous marls which have locally been disturbed by tepee structures formed during desiccation and are interbedded with sand lenses. Unit 9 (also referred to as Ti's al Ghadah Lake Surface [TLS] in *Chapter Four*) is the youngest deposit in the sequence and comprises a sand bed that expresses a contorted/deformed relationship with the underlying marls. Units 5 and 9 are the most abundant in fossil mammal remains.

The marls represent carbonate precipitation and deposition within a lacustrine environment and this unit is used as evidence for the existence of a humid phase at this point in the stratigraphy. This is suggested as the formation of a permanent water body at a locality underlain by well-drained aeolian sands requires an increase in mean annual rainfall and the elevation of the regional groundwater table. No *in situ* fossils have been recovered from Units 6–8, which means none of the remains discussed here come from the sedimentary unit with the most diagnostic evidence for humid conditions. It is important to stress, however, that the sedimentology of Units 5 and 9 indicate that these were also likely to have been deposited during a humid phase. The presence of clasts and root traces within Unit 5 indicate that this deposit was waterlain by sheet flow operating across a vegetated surface, while the green colouration suggests that a high-water table and anoxic conditions would have existed during the deposition of this unit.

The sands of Unit 9 express a conformable relationship with the underlying marls with respect to the deformation and convolution of the contact between these units. This implies that the marl units were still relatively wet and unconsolidated when the sands of Unit 9 were laid down. Consequently, although no fossils have been found within the most diagnostic lacustrine deposits at Ti's al Ghadah, the sedimentology of the fossil rich units (i.e. Units 5 and 9) is indicative that these sediments were also laid down during a humid phase. It is, therefore, likely that Unit 5 and 9 were deposited early and late in the humid phase respectively as they occur above and below the marl beds that represents the period of most extensive lake development. This suggestion is also supported by the environmental tolerances of the taxa present in the fossil assemblages that indicate the persistence of wet conditions during their accumulation.

Fossils are well-preserved in Unit 5 and include an abundance of small and fragile bird and reptile remains. Very few bones display abrasions or rounding suggesting limited hydraulic influence in the accumulation of the assemblage (Stimpson et al., 2016). Trampling was evident in the form of breaks and fine striae on the surfaces of bones, but overall evidence for trampling is limited. Weathering is low to moderate suggesting that burial was rapid (Stimpson et al., 2016). Some fossils display higher weathering stages, maximally to Behrensmeyer's (1978) weathering stage 4, and were likely exposed to subaerial weathering processes for at least six years. Carnivore tooth pit size – in conjunction with faunal remains – implicate both small- and large-bodied carnivores in the accumulation of the fossil assemblage. It is possible that small carnivores (e.g. Vulpes), and carnivorous birds (e.g. Neophron percnopterus), were attracted to the lake to scavenge from large carnivore refuse (Stimpson et al., 2016). Carnivore gnawing ranged from 0% to 4.3% depending on skeletal element, and ribs were the most intensely ravaged element (Stimpson et al., 2016).

The relationship between lithic artefacts reported previously in the basin and the fossil deposits from Unit 5 has remained unclear. Scerri and colleagues (2015) reported the recovery of 76 artefacts from the surface at Ti's

al Ghadah. These were focused in two areas below and beside the main sedimentary ridge at the site (see also *Chapter Four*). The artefacts were described as being of Middle Palaeolithic character, with possible indications of a specifically early Middle Palaeolithic attribution. Broad similarities with the Yabrudian were also noted, given factors such as the seemingly low frequency of Levallois technology. It should be noted that no large cutting tools (e.g. hand axes) have been recovered from the basin.

Optically Stimulated Luminescence (OSL) dating of the palaeolake and sandy sediments associated with the fossil fauna returned ages of 291 ± 34 ka and 318 ± 24 ka to 328 ± 36 ka, respectively (Rosenberg et al., 2013; Stimpson et al., 2016). Uranium-series dating of bovid fossil tooth enamel and dentine produced ages ranging from *c*. 350-230 ka, while combined U-series and Electron Spin Resonance (ESR) dating of fossil tooth enamel yielded ages of $473 \pm 50/-33$ ka and $554 \pm 79/-76$ ka (Stimpson et al., 2016). The available dates suggest an age of approximately *c*. 500-300 ka for Unit 5, with Stimpson et al. (2016) suggesting *c*. 500 ka as the most probable age given the minimum, combined direct U-series and ESR ages on fossil tooth enamel (Table 1). Given that the main aim of this paper was to reconstruct palaeoenvironmental conditions associated with middle Pleistocene hominin occupation of the for Nefud Desert, however, we use the age range throughout the paper for consistency.

Given all this sedimentological, chronological, and taphonomic information, the fossiliferous sands of Unit 5 likely represent dunes that became stabilised by vegetation at the start of a humid phase and exposed to overland flow and groundwater processes. The overlying lacustrine sediments would have formed later on in this humid phase, when the lake reached its maximum extent. Under this scenario the fossil assemblage recovered from Unit 5 represents the remains of animals that died on the margins of the basin centre lake and were buried soon after when the lake waters expanded over the sands.

METHODS

Bone surface modification and lithic analysis

The lithic material and debitage was measured, recorded, and drawn following previously published protocols (Scerri et al., 2014). Fossil identification and analysis was conducted at the Australian National University (ANU) and the University of New South Wales (UNSW), Australia, and facilitated by comparative osteological material. Each specimen was examined by eye and hand-lens (10 - 20x) and at different angles to identify fine-scale surface modifications that only become apparent at certain angles of light exposure. Bone surface modifications, such as tooth and percussion marks, were analysed and recorded following standard methodologies for taphonomic analysis of fossil faunal assemblages (e.g. Capaldo and Blumenschine, 1994; Fisher, 1995).

Cut marks were defined as V-shaped grooves that are often accompanied with features such as shoulder effect, flaking, and microstriations (Domínguez-Rodrigo et al., 2009), and were considered when analysing modifications in this study. Markings suspected of being cut marks were further inspected by Scanning Electron Microscopy (SEM). A Hitachi S-3400N scanning electron microscope operated in variable-pressure mode (VP-SEM) was used to capture backscatter (BSE) images of the sample surfaces. The large chamber accommodated the large specimens and specimens were mounted on SEM stubs using Leit-C-PlastTM carbon-based removable adhesive.



Figure 2. Stratigraphic log and available chronological information for Ti's al Ghadah focused on the main fossilbearing layer of Unit 5. Adapted from Stimpson et al. (2016).

Table 1. Accepted Ti's al Ghadah chronological information available from Optically-stimulated luminescence (OSL), Uranium-thorium (U-series) and Electron Spin Resonance (ESR) methods as reported by Rosenberg et al. (2013) and Stimpson et al. (2016). Full methods and criteria of acceptance can be found in Rosenberg et al. (2013) and Stimpson et al. (2013) and Stimpson et al. (2013).

Sample	Method	Material	Unit	Age (ka)	Reference
C17.1/1	OSL	Sand/quartz	5/4?	318 ± 25	Rosenberg et al. 2013
C17.1/1	OSL	Sand/quartz	5/4?	328 ± 36	"
TAG1- OSL4	OSL	Sand/quartz	7	291 ± 34	Stimpson et al. 2016
3536	U-series	Tooth enamel	5	251 ± 25	n
3536	ESR	Tooth enamel	5	473 +50/-33	"
3538	U-series	Tooth enamel	5	235 ± 9	"
3538	ESR	Tooth enamel	5	554 +79/-76	"

Notches were defined as circular to semi-circular breaks in the edge of midshaft fragments and are typically produced by both hominins and large carnivores when exploiting within bone nutrients (i.e. marrow) (Capaldo and Blumenschine, 1994). Dynamic loading forces associated with hammerstone percussion tend to produce notches that are wider and shallower than those generated by carnivores, allowing notches to be quantitatively differentiated. Notch morphology was determined following the protocol described in Capaldo and Blumenschine (1994) and notches were compared to those generated by carnivores, un-modified hammerstones, and modified hammerstones under experimental settings (Capaldo and Blumenschine, 1994; Galán et al., 2009).

Fourier-Transform infrared spectroscopy

Tooth enamel preservation was assessed by means of Fourier Transform Infrared Spectroscopy. Although reliable δ^{13} C- and δ^{18} O-based dietary and environmental indicators have been demonstrated across millions of years (Lee-Thorp et al., 1989), protocols to check the structural preservation of fossil tooth enamel samples remain important. This is particularly the case in tropical forest environments with ion rich soils and high hydrological activity. One means to check enamel preservation is the application of Fourier Transform Infra-red Spectroscopy (FTIR), which absorbs radiation at discrete vibrational frequencies related to the presence environment of key functional groups. and crystallographic The $(PO_4^{3-}),$ polyatomic of phosphates ions interest are carbonates (CO_3^{2}) , and hydroxyl groups (OH). The observed absorbance bands of enamel can be ascribed to the internal vibrations of these molecular groups (Farmer, 1974; LeGeros, 1991).

We use the empirical indices used by Sponheimer and Lee-Thorp (1999), Roche et al. (2010), and Roberts et al. (2017) to characterize the crystal-chemical properties of enamel bioapatite. The possible presence of calcite was assessed in all samples by checking for a peak at 711 cm⁻¹ (Sponheimer and Lee-Thorp, 1999; Lee-Thorp and van der Merwe, 1991). Ten fossil faunal samples from Unit 5 were compared to ten modern enamel samples prior to any pre-treatment in order to determine the potential for diagenetic structural and compositional modification of enamel during burial (Appendix A, Table S9). Mann-U-Whitney tests were performed for each of

the main FTIR indexes of enamel bioapatite (PCI, PO₄RF, BPI, API, and WAMPI – as per Roche et al., 2010) in order to determine statistical differences in enamel crystallinity and structure between fossil and modern samples. All statistical analyses were conducted using the free program R software (R Core Team, 2013).

For all samples, powdered enamel was analysed between 400 and 4,000 cm⁻¹ by FTIR spectroscopy with Attenuated Total Reflectance (FTIR-ATR – Agilent Technologies Cary 640 FTIR with GladiATRTM from Pike Technologies). Each sample was measured three times. The background was subtracted, and a baseline correction was carried out using Agilent Resolution Pro software. The baselines of the spectra were normalized, and all three spectra of each sample were averaged before calculation of the various infrared indices. To ensure better reproducibility of the measurements, only spectra with a minimum absorbance of 0.06 for the highest phosphate band at ~1035 cm⁻¹ were taken into account. The reproducibility of the indices BPI, API, BAI, and PCI are ± 0.01 , ± 0.004 , ± 0.1 and ± 0.1 , respectively.

Stable carbon (δ^{13} C) and oxygen (δ^{18} O) isotope analysis

Twenty-one samples were selected for δ^{13} C and δ^{18} O isotope analysis of tooth enamel from the available fossil material from Unit 5 at Ti's al Ghadah. All teeth that could be confidently identified, as well as excavations by the Saudi Arabian Geological Survey in 2011 (Appendix A, Table S1), were sampled. Fossil *Equus* sp. (*n*=4), *Palaeoloxodon recki* (*n*=2), and *Alcelaphus* sp. (*n*=1) were targeted for δ^{18} O measurement as abundant obligate drinkers, while *Oryx* sp. (*n*=10) comprise the non-obligate drinker sample from the site. Second and third molars were targeted, although not all teeth can be confidently said to have come from separate individuals and, therefore, the data may include some interindividual variability. 'Drinker' categorization was based on observations of the ecological behaviours of closely related species (Kingdon, 1997; Grinder et al., 2006; Rubenstein, 2010). It should be noted, however, that while *Alcelaphus* drinks often when water is available, populations from the arid Kalahari are known to obtain significant portions of their water intake from melons and underground storage organs (Kingdon, 1997).

To provide a modern baseline estimate of aridity in Saudi Arabia for these taxa, $\delta^{18}O$ measurements were made on modern equids (Equus caballus) (n=4) and camels (Camelus dromedarius) (n=2) reliant on oasis water and compared to the $\delta^{18}O$ of modern samples of Arabian oryx (O. *leucoryx*) (*n*=7). Modern oryx samples were obtained from the fenced Mahazat as-Sayd Protected Area in central Saudi Arabia and associated with a mass mortality event during a severe drought in 2007 (Zafar-ul Islam et al., 2010) (Appendix A, Table S2). Modern equid and camel specimens were retrieved from oases within 10 kms of the site of Ti's al Ghadah in 2013 and 2014. Local informants stated that these animals had grown up as feral and died due to a lack of natural water, as they were reliant on oases rather than local wells. They may have had access to local crops and fodder, however. Annual climate data from the Al Muwayh monitor station 15 kilometres north of the Mahazat al-Sayd Protected area and from the Ha'il monitor station in the vicinity of Ti's al Ghadah document mean annual temperature and mean annual precipitation during the years of death of the non-obligate and obligate drinkers (Table 2). A survey of precipitation across the western Arabian Peninsula between 1989 and 1992 indicated a δ^{18} O (Vienna Standard Mean Ocean Water, VSMOW) range of between c. -2.9 and -0.5%, though it should be borne in mind that this data is seasonal and from two decades prior to the collection of the modern samples analysed here (Alyamani, 2001).

We also selected five Oryx, three Equus, and two Palaeoloxodon recki teeth for additional, sequential analysis based on their completeness and robustness to endure additional sampling (Appendix A, Tables S1 and S3– S5). The five fossil Oryx teeth were, in turn, compared to one modern Oryx*leucoryx* specimen (Appendix A, Tables S2 and S6) in order to provide a modern baseline for seasonal changes in δ^{18} O in this non-obligate drinker.

All teeth were cleaned using air-abrasion to remove any adhering external material. Enamel powder for bulk analysis was obtained using gentle abrasion with a diamond-tipped drill along the full length of the buccal surface in order to ensure a representative measurement for the entire period of enamel formation. For sequential samples, each sample was a 1–2 mm wide groove perpendicular to the tooth growth axis, through the thickness of the enamel layer. The distance of the base of each sample groove from the enamel/root junction from the furthest sample margin was recorded.

All enamel powder was pre-treated to remove organic or secondary carbonate contaminates. This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified H₂O and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified H₂O (as per Sponheimer et al., 2005; Lee-Thorp et al., 2012). Following reaction with 100% phosphoric acid, gases evolved from the samples were analysed to stable carbon and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for the Science of Human History. Carbon and oxygen isotope values were compared against international standards (NBS 19, MERCK) registered by the International Atomic Energy Agency. Replicate analysis of OES standards suggests that machine measurement error is $c. \pm$ 0.1‰ for δ^{13} C and \pm 0.2‰ for δ^{18} O. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard ($n=20, \pm 0.2\%$ for $\delta^{13}C$ and $\pm 0.3\%$).

Table 2. Annual mean temperature (AMT) and annual average precipitation (MAP) for the modern sites used in this study. Data for East African sites comes from Blumenthal et al., 2017.

Site	Country	AMT (°C)	MAP (mm)
Ti's al Ghadah	Saudi Arabia	22.9	9
Mahazat as-Sayd Protected Area	Saudi Arabia	25.6	120
Laikipia	Kenya	21.8	640
Tsavo	Kenya	25.0	549

In this paper we use the standard fossil fuel effect of 1.5‰ correction that takes into account changing δ^{13} C of atmospheric CO₂ during the industrial revolutions (Francey et al., 1999; Zachos et al., 2001). While additional changes in atmospheric CO₂, as well as shifts in pCO₂, are possible (Levin et al., 2008; Hare et al., 2018), they are not well understood beyond the Last Glacial Maximum and are not likely to, together, exceed 0.5‰ (Calvin and Benson, 1948; Hare et al., 2018). As a result, we do not consider these here.

The relationship between δ^{18} O and Site and Group (obligate and non-obligate drinkers) was determined using a mixed Site*Group ANOVA comparative test, followed by post-hoc Tukey pair-wise comparisons. Statistical regression analyses were undertaken to discern the statistical correlation between δ^{13} C and δ^{18} O at Ti's al Ghadah. All statistical analyses were conducted using the free program R software (R Core Team, 2013).

RESULTS

Preliminary bone surface modification and lithic analysis

A total of 1929 fossil specimens were recovered from Ti's al Ghadah and preliminary results of the taphonomic analysis are presented here (see *Chapter Four* for a detailed taphonomic analysis of this assemblage). Medium-sized ungulates are the most common, and most of these are attributable to *Oryx* sp. Carnivore damage included scores, pits, punctures, and furrowing of epiphyses, and was found on 17.1% of all bones, with ribs (26.7%) and midshafts (17.1%) representing the most intensively ravaged elements. Tooth-marked midshafts suggest carnivores probably had, at least on occasion, primary access to fleshed carcasses. Large tooth pits and tooth notches on midshaft fragments indicate that carnivores, likely hyena, were gaining access to marrow.

In addition, associated faunal material includes two medium-sized ungulate rib fragments that bear tentatively assigned cut marks (TAG13/133 and TAG13/900; Figs. 3D and E). The internal appearance of the cut marks is similar to the overall cortical surface and pitting from sand grains clearly overlays the groove supporting their antiquity. These markings are V-shaped in cross-section and run parallel to each other and either perpendicular or obliquely to the long axis of the bone. Shoulder effect and shoulder flaking is apparent, the latter in the form of Hertzian cones. No internal microstriations were observed, although fine-scale features, such as microstriations, are quickly removed during chemical alteration (Pineda et al., 2014). The direction and location of the markings is consistent with cut marks produced during filleting of meat from around the rib (Pickering et al., 2013).

Notches with a broad arcuate planform and conchoidal medullary flake scar, reminiscent of notches produced during hammerstone percussion, were also identified and suggest hominins may have broken open long bones to exploit marrow. A single complete notch (TAG13/121; Fig. 3B) was located on the medial side of a proximal metacarpal of a medium-sized bovid and the notch dimensions place this within the 95% CI range of notches produced by modified hammerstones and is outside the range of any carnivore produced notches (Fig. 4). The specimen exhibits an oblique and curved fracture pattern, indicating that the bone was broken while fresh. There are no carnivore tooth marks, the cortical surface exhibits a flake scar with an adjacent wide striae field, and an adhering bone flake to the medullary, all of which are suggestive of hammerstone percussion. An arcuate and shallow notch (TAG14/9235; Fig. 3C) was identified on a tibia shaft fragment and the notch dimensions fall within those produced by non-modified hammerstones and carnivore gnawing on non-metapodial limb bones. An indeterminate straight, narrow V-shaped groove runs roughly parallel to the long axis of the bone. The groove terminates in a shallow fork at one end, a trait often found in cut marks produced by retouched tools (Domínguez-Rodrigo et al., 2009), but lacks other features typically associated with cut marks (e.g. shoulder flaking and microstriations). A third incomplete notch (TAG14/9254) shows clear signs of fresh breakage and percussion pits with associated striae and was found alongside a bone flake clearly resulting from dynamic loading. Other similar bone flakes were recovered, and in one case (TAG13/9133; Fig. 3G) pits reminiscent of percussion pitting are clearly visible on the cortical surface.

In addition to the faunal remains, six unretouched flakes and one retouched flake were recovered from Unit 5 (Fig. 3A). A further six chunks were recovered with the artefacts and likely represent highly fragmented debitage. The lithics and debitage fragments are made on a brown coloured lacustrine chert, and this material is known from lakebeds across the Nefud (Groucutt et al., 2015, 2018 Breeze et al., 2016). At the MIS 5 site of Al Wusta, 3km from Ti's al Ghadah, similar lacustrine chert was the main raw material used by hominins (Groucutt et al., 2018). Despite difficulties in knapping such material, the artefacts are finely made and similar to one another in terms of technology. The lithics consist of small flakes struck from prepared cores and a side-retouched flake ('side scraper').



Figure 3. A) chert flakes with dihedral striking platforms (i, iii and iv) and a side retouched flake (ii). B) medium-sized bovid proximal metacarpal (TAG14/121) in cortical (i) and medullary (ii and iii) view. In the inset a wide striae field (white box) is visible adjacent the flake scar (dashed line). A adhering bone flake (arrow) and conchoidal flake scar (dashed line) are visible from the medullary. The refitted piece (iii) exhibits a smooth, oblique fracture pattern indicating the bone was broken while fresh. C) a tibia shaft fragment (TAG14/9235) in cortical (i) and medullary (ii) view. An indeterminate narrow, V-shaped groove with a forked end (arrows) runs parallel to the long axis of the bone. A conchoidal flake scar is present on the medullary surface

(dashed line). D) dorsal view (i) of a medium sized mammalian rib fragment (TAG13/900) with two probable cut marks that run obliquely to the long axis of the rib. Shoulder effect (arrows) is clearly visible in the SEM image (ii). E) a medium-sized mammalian rib fragment (TAG13/133) with multiple parallel grooves running perpendicular to the long axis of the bone and shoulder effect in the form of Hertzian cones (triangles) that are clearly visible in the SEM image (ii). F) a medium-sized bovid metapodial shaft fragment (TAG14/9257) in cortical (ii) and medullary (ii) view with multiple opposing notches and conchoidal flake scars (dashed lines), and numerous carnivore tooth scores (arrows), suggesting the bone was broken open by a large carnivore. G) medium size mammalian shaft bone flake (TAG13/9134) in medullary (i) and cortical (ii) view. Smooth and oblique fracture pattern indicates the bone was broken while fresh and likely by a dynamic force. The surface exhibits pitting (arrows) and the bone flake has tentatively been attributed to be the result of hammerstone percussion. Solid scale bar = 20 mm. Dashed scale bar = 0.5mm

Figure 4 (below). Morphology of notches produced by hammerstone percussion and carnivore gnawing on long bones of medium-sized ungulates. Measurements taken following the protocol described in Capaldo and Blumenschine (1994). Rectangles represent 95% CI ranges. Dashed rectangles represent experimental carnivore and hammerstone percussion notches on metapodial and non-metapodial long bones (data from Capaldo and Blumenschine, 1994). Grey-shaded rectangle is simply for ease of viewing. Solid rectangles represent experimental carnivore and percussion notches produces by modified and non-modified hammerstones (data from Galán et al., 2009). Note that solid rectangles include both meaty (nonmetapodial) and non-meaty (metapodial) long bones. Star, square and circle represent TAG13/121, TAG14/9235, TAG13/9257 respectively.



Fourier-Transform infrared spectroscopy

Full results of the infrared indices of samples subjected to FTIR analysis are shown in Appendix A, Table S9. All of the fossil and modern enamel samples displayed classic enamel FTIR spectra (see Appendix A, Fig. S1). No additional bands from secondary carbonate (e.g. calcite at 711cm⁻¹) were observed in the spectra of the fossil samples. Mann-U-Whitney tests showed no significant difference in B-site carbonation between modern faunal and fossil faunal groups (W=53.5, p>0.05) (see Appendix A, Fig. S2). Fossil mammalian enamel demonstrates A-site de-carbonation (W=18.5),dehydration and organic decay (lower WAMPI) (W=0.6, p<0.05), and higher BAI (W=95.5, p<0.05) relative to modern mammal samples, as observed elsewhere (Roche et al., 2010; Roberts et al., 2017; Lee-Thorp and van der Merew, 1991; Sponheimer, 1999).

A loss of water organic content (as indicated by WAMPI) is expected over multimillennial time-scales, particularly in tropical areas with limited organic preservation. Given API and WAMPI reduction, alongside BPI stability, in fossil mammal samples, the primary mechanism of BAI change in this instance is likely endogenous carbonate loss at A-sites linked to organic degradation (Sponheimer, 1999; Roche et al., 2010; Roberts et al., 2017). Fossil mammalian tooth enamel also showed an increase in PCI (W=90.0, p<0.05) compared to modern mammalian tooth enamel. This increase in crystallinity and organization is a common process of fossilization as organics are removed (Sponheimer, 1999; Sponheimer and Lee-Thorp, 1999; Roche et al., 2010).

To summarise, the fossil enamel FTIR spectra produced here are virtually indistinguishable from modern spectra. The precipitation of carbonate minerals is likely to be more of a problem in the context of more porous materials such as dentine and bone (Lee-Thorp and van der Merwe, 1991; Sponheimer, 1999; Lee-Thorp, 2008; Roche et al., 2010; Roberts et al., 2017). Subtle differences noted in faunal enamel apatite during fossilization, including increased BAI, decreased WAMPI, and decreased A-carbonate on phosphate index, appear to be linked to the reduction in organic material within the apatite matrix through time. Increased PCI and crystallinity are associated with increased order as a result of fossilization. Such change is not considered to have major impacts on overall enamel apatite structure or stable carbon and oxygen isotope measurements from enamel (Sponheimer, 1999; Roche et al., 2010; Roberts et al., 2017).

Stable carbon (δ^{13} C) and oxygen (δ^{18} O) isotope analysis

The δ^{13} C data from all of the sampled fossil mammals (*Palaeoloxodon*, *Oryx*, *Alcelaphus*, *Equus*, and unidentified bovids) show an unequivocal dominance of C₄ vegetation in the diets of herbivores (δ^{13} C range = -0.8 to 3.3‰) (Fig. 5; Appendix A, Table S3) and suggests that rainfall occurred during the warm season. The δ^{13} C evidence also fits with climate simulations suggesting that the periodic climatic amelioration of Arabian environments reflects the incursion of the African monsoon system (Jennings et al., 2015). The uniformity of C₄ consumption by all animals suggests the presence of extensive, productive C₄ grasslands in the vicinity of the palaeolake. The δ^{18} O range of fauna from Ti's al Ghadah is high (δ^{18} O range = -5.6 to 6.2‰) – though not higher than Pliocene, Pleistocene, and contemporary African ecosystems (Sponheimer and Lee-Thorp, 1999, 2001; Levin et al., 2006; Blumenthal et al., 2017).

Modern *Oryx* show a similar reliance on C₄ grasses with δ^{13} C values of -3.9 to -0.1‰. Here, it should be remembered that one must add 1.5‰ onto modern samples to bring them in-line with pre-industrial atmospheric CO₂ δ^{13} C. This would lead to a modern range of -2.4 to 1.4‰, that approximates that of the fossil *Oryx* sp. Such results are consistent with the grasslands available at the Mahazat as-Sayd Protected Area. The modern *Equus* and *Camelus* have a δ^{13} C range of -9.6 to -5.9‰ (or -8.1 to -4.4‰) that indicates a significant input of C₃ resources into their diets. Given that the modern environment of this region supports arid shrubs and succulents, with no grasses, this likely either indicates access to local C₃ crops, C₃ sedges near oases, or CAM succulents with similar values to C₃ plants, or a combination of the three. Given the feeding preferences of these animals, access to crops seems like the most probable source of this C₃ signal. Importantly, as this shift in diet is only seen in the obligate drinkers, this will have no impact on the interpretation of δ^{18} O through time that will primarily reflect the available open water sources to the obligate drinkers, rather than food source.



Figure 5. δ^{13} C and δ^{18} O measurements from the tooth enamel of fossil fauna from Ti's al Ghadah, Saudi Arabia, analysed in this study. VPDB, Vienna PeeDee Belemnite.

The δ^{18} O range of fauna from Ti's al Ghadah (-5.6 to 6.2‰) is much lower than that of the modern fauna sampled (-3.6 to 10‰). The source of this variation becomes clearer when we compared obligate and non-obligate drinkers separately. The δ^{18} O range of modern obligate drinkers (-3.6 to 1.8‰) is broadly similar to that of fossil obligate drinkers (-5.6 to 0.9‰). By contrast, the δ^{18} O of modern non-obligate drinkers (1.3 to 10.0‰) is elevated when compared to that of fossil non-obligate drinkers (-1.6 to 6.2‰). As a result, δ^{18} O changes seen between the fossil and modern assemblage can be primarily linked to changes in non-obligate drinker δ^{18} O. Given our knowledge of the connection between these animals and changing plant evapotranspiration and water stress, this implies differences in aridity through time. The efficacy of this comparison is also highlighted by the more acute seasonal changes in obligate drinkers versus nonobligate drinkers at Ti's al Ghadah (Fig. 7 and 8).

This is further evidenced when we compare the medians between non-obligate and obligate drinkers in the modern dataset versus the fossil dataset. The δ^{18} O difference (non-obligate drinker median = 0.0‰, obligate drinker median = 1.7‰, difference = 1.7‰) between obligate and non-obligate fossil taxa is 6.0‰ lower than that found between modern *Equus/Camelus* (median = 0.7‰) and *Oryx leucoryx* (8.4‰) in central Arabia today (difference = 7.7 ‰), demonstrating that conditions were considerably wetter in the region's past. This remains the case even when *Palaeoloxodon* and *Alcelaphus* are removed from the fossil sample. The unidentified bovids were not included in the fossil sample since the bovids could not be definitively identified as obligate or non-obligate drinkers (Appendix A, Table S1) and this also facilitated the most reliable comparison in terms of body size and taxa with our modern datasets.

This difference is compared to δ^{18} O datasets of obligate drinking and non-obligate drinking mammals in present day East Africa (Fig. 6; Table 2) (Blumenthal et al., 2017). We used only Bovidae, Equidae, and Elephantidae from their dataset to increase comparability and focused on the two sites (i.e. Laikipia and Tsavo) with detailed water deficit information and a sample size of >5 of both obligate and non-obligate drinkers (Blumenthal et al., 2017). While caution is warranted given that taxon-specific habits could vary through time, when the difference between obligate and nonobligate drinker δ^{18} O from Ti's al Ghadah is compared to that of modern day Tsavo (1.7‰) and Laikipia (1.3‰), middle Pleistocene ecological conditions in the interior of Arabia appear to approximate that of a relatively humid African savanna today (Fig. 6).



Figure 6. δ¹⁸O values for non-obligate and obligate drinking taxa at the East African localities of Laikipia (Kenya) and Tsavo (Kenya) reported by Blumenthal et al. (2017), for modern Saudi Arabia, and for the middle Pleistocene Ti's al Ghadah assemblage. Boxes show the median and the lower (25%) and upper (75%) quartiles; whiskers encompass all data points within 1.5x the interquartile range of the box. VPDB, Vienna PeeDee Belemnite.

The relationship between δ^{18} O and Site and Group (obligate and non-obligate drinkers) was tested using a mixed Site*Group ANOVA comparative test, followed by post-hoc Tukey pair-wise comparisons. A difference between the δ^{18} O of the two groups by site is demonstrated by the test (F(1,129)=43.853, p<0.05), highlighting the utility of the comparison as an environmental index. When pairwise comparisons are performed on a site-by-site basis, obligate and non-obligate drinker δ^{18} O is not significantly different at Laikipia and Tsavo (F(3,129)=9.186, p>0.05). There is a significant difference between these groups at Ti's al Ghadah, perhaps related to the relatively small sample size, and in the modern Saudi Arabian dataset (F(3,129)=9.186, p<0.05) (Appendix A, Tables S7–S8).

There is no correlation between the δ^{13} C and δ^{18} O values in the Ti's al Ghadah fossil dataset (Multiple R-squared=0.04, p<0.01, adjusted Rsquared=-0.01, p<0.01), indicating that access to vegetation was independent of factors affecting faunal δ^{18} O. This is also borne out in sequential δ^{13} C and $\delta^{18}O$ analyses of selected fossil teeth that enables the identification of potential environmental seasonality or mobility. The sequential $\delta^{13}C$ data, from all taxa, document a homogeneous source of lush C₄ vegetation, likely in the form of grasses, at Ti's al Ghadah (Fig. 7-8; Appendix A, Tables S3 and S5). This could either be linked to the persistence of C_4 vegetation in the western Nefud Desert or animal movements tracking seasonal availability of C_4 resources. Sequential $\delta^{18}O$ provided more insights in this regard and *Oryx* sp. $\delta^{18}O$ documents clear, sigmoidal fluctuations usually associated with seasonal variations in regional environmental conditions rather than use of different water sources (Sponheimer, 1999; Balasse, 2002) - in this case seasonal variation in the evaporative stresses placed on plants consumed (Fig. 7). Similar, although dampened, sigmoidal curves can also be seen in the equid individuals sampled, suggesting seasonal changes in the level of evaporation affecting the drinking water imbibed by these individuals (Fig. 8). These results are consistent with environmental seasonality in ranges covered by the two taxa sampled. Furthermore, the difference in the degree of acuteness of these seasonal changes between the *Oryx* sp. and equids further highlights the validity of using the relative magnitude δ^{18} O distinctions between non-obligate and obligate drinking taxa as a palaeoaridity indicator.

The two P. recki specimens demonstrate very little variation in either δ^{13} C or δ^{18} O through the formation of the tooth, suggesting reliable access to stable water bodies and C₄ grasses (Fig. 8). Given documentation of seasonal patterns in $\delta^{18}O$ in Oryx sp. and equids with more limited ranges, the fact that P. recki documents limited changes suggests that these animals were migrating over much larger distances, perhaps following lake and river systems with relatively similar δ^{18} O values. Furthermore, geomorphological insights have also suggested that the Ti's al Ghadah palaeolake would have been relatively shallow, further suggesting that P. recki had to range to obtain enough water throughout the year. The potential undertaking of significant, long distance migrations in search of water and vegetation would fit with the behaviours documented among African elephants today (Cerling et al., 2006). Furthermore, such results are also compatible with suggestions based on palaeolake and palaeoriver modelling, using Geographical Information Systems, that indicate that Ti's al Ghadah was not an isolated oasis, but rather part of a broader, often interconnected, chain of palaeolakes during wet intervals (Breeze et al., 2016).



Figure 7. Sequential δ^{13} C and δ^{18} O measurements for *Oryx* sp. samples TAG 1551, TAG 549 1541, TAG 149, TAG 942, and TAG 944 from the middle Pleistocene levels of Ti's al Ghadah and one modern *Oryx leucoryx* sample from the Mahazat as-Sayd Protected Area. VPDB, Vienna PeeDee Belemnite.



Figure 8. Sequential δ^{13} C and δ^{18} O measurements for equid samples SGS180, SGS57 and SGS1094 and *Palaeoloxodon recki* samples TAG14 301 and TAG14 129 from the middle Pleistocene levels of Ti's al Ghadah. VPDB, Vienna PeeDee Belemnite.

DISCUSSION

The recovery of unambiguous hominin-produced lithic material, in association with evidence from the fossil record suggestive of hominin butchery activities, reported here and dated to c.500 - 300 ka, represents the oldest dated hominin occupation in Arabia. While the small sample size makes detailed descriptions of the assemblage's lithic technology and cultural attributions currently difficult, they demonstrate a middle Pleistocene hominin presence in Arabia. It is considerably older than the previously oldest site of Jebel Qattar-1 at c. 210 ka (Petraglia et al., 2012) and, alongside recent research (Ignaccio et al., 2018), highlights the benefits of systematic, detailed taphonomic study of fossil material when exploring hominin arrival in different parts of the world. In addition to recent finds of H. sapiens in the Arabian interior c. 90 ka (Groucutt et al., 2018), the Ti's al Ghadah evidence highlights that focus on Pleistocene Homo expansions should not solely be limited to Eurasia, Africa, and the Levant. The identification of Afro-tropical, Saharao-Arabian, and Palearctic fauna (Thomas et al., 1998; Stimpson et al., 2015, 2016; Stewart et al., 2017) in association with a hominin presence also highlights the possibility of middle, and perhaps also early, Pleistocene hominin migrations into the Arabian Peninsula from Africa and Eurasia. Future systematic survey and excavation will help to further constrain the chronology and nature of hominin dispersal into this part of the world.

The stable isotope data from fauna directly associated with these traces of hominin activity at Ti's al Ghadah provide detailed insights into palaeoaridity and palaeovegetation in this part of Arabia during periods of hominin migration. A substantial corpus of environmental data exists for the late Pleistocene documenting recurrent humid episodes (Parker, 2010; Drake et al., 2013; Parton et al., 2015; Breeze et al., 2016), although generally deficient knowledge of evapotranspiration and insufficient on-the-ground testing of the results of climate change models has led to limited understanding as to what 'wetter' represents in the context of regional vegetation and biomass. Meanwhile, modern Arabian landscapes, to which we might look for analogues, have been heavily modified by Holocene anthropogenic activity. The situation is even worse for the middle Pleistocene. As shown in Table S10 (see Appendix B), the majority of these three proxies are from three locales (i.e. the Hoti and Al Mukalla caves in Oman and Yemen, and the alluvial fan complexes of the Hajar mountains). Only a few exist for northern Arabia, demonstrating the importance of the Ti's al Ghadah assemblage for studying environmental conditions associated with hominin incurrences.

The data presented here highlight the presence of abundant C₄ grasslands and aridity levels somewhat similar to those found in East Africa today. The comparison of obligate and nonobligate drinker stable oxygen isotopes has been little-developed beyond Africa, yet we hope to have shown here that this methodology could and should be applied to other parts of Asia, such as the Thar Desert, central Asia, and eastern Asia in order to develop more detailed understandings of hominin adaptations to semi-arid and arid environments in these parts of the world. The data reported here also fits with palaeoecological reconstructions based on the fossil taxa identified at Ti's al Ghadah (Thomas et al., 1998; Stimpson et al., 2015, 2016; Stewart et al., 2017). It has been shown that herbivore biomass and richness positively correlate with net primary productivity (NPP) and rainfall across a range of environments (e.g. Coe et al., 1976; Thackeray, 1980; Faith, 2011). Thackeray (1980), for example, found that ungulate biomass and richness was greater in areas of elevated productivity and rainfall in southern Africa, and argued

that such data could be used as a proxy for primary productivity in archaeological and palaeontological contexts. Therefore, the isotopic data, coupled with a richer and larger herbivore community at Ti's al Ghadah, as indicated by the fossil record (e.g. *Palaeoloxodon*, alcelaphines), strongly indicate the presence of more productive and expansive grasslands than found in the region today. Moreover, the presence of fish and birds with strong affinities toward water (e.g. Anas and Tachybaptus) imply the presence of large perennial water sources (Thomas et al., 1998; Stimpson et al., 2015, 2016; Stewart et al., 2017), while the presence of a large felid (Panthera sp. cf. P. gombaszoegensis) and hyena indicate that the western Nefud Desert was also host to a substantial prey-biomass (Thomas et al., 1998; Stimpson et al., 2015, 2016). Alongside evidence from sequential isotopic analysis of the wide-ranging P. recki reported here, attainment of lake sequences should also help to clarify wider, regional environmental trends during the earliest arrival of hominins into Arabia. Overall, early and middle Pleistocene hominin populations would seemingly have been able to extend not only into the Levant, but also deep into the Arabian Peninsula, potentially making use of access to a combination of African and Eurasian medium- and large-sized mammals, as well as similar grassland habitats (Martínez-Navarro, 2004; Dennell and Roebroeks, 2005; Stewart et al., 2017).

The identification of late Pleistocene *H. sapiens* and middle Pleistocene hominins in the interior of the Arabian Peninsula opens the possibility of exploring the adaptive capacities of different hominin taxa in what is, today, an extreme environment. The proto-global distribution of non-*H. sapiens* middle Pleistocene *Homo*, as well as growing evidence for its cultural capacity (Joordens et al., 2016; Hoffman et al., 2018), have been argued to represent a potential adaptive threshold, demonstrating the exploitation of new environments (e.g. Morwood et al., 1998; Potts, 2013). In
line with previous suggestions (Stewart et al., 2017), we demonstrate that middle Pleistocene hominin expansions into this region would not necessarily have required new innovations or adaptations to harsh desertic aridity and imply a range expansion similar to other large- and medium-sized mammal populations moving between Africa, the Levant, and Eurasia. By contrast, although our own species was also reliant on periods of increased precipitation to access the Arabian Peninsula (Groucutt et al., 2018), it appears to have had a wide geographic spread (Armitage et al., 2011; Delagnes et al., 2012; Breeze et al., 2017; Groucutt et al., 2018), penetrating further into the dune fields and living under conditions that were perhaps harsher than their middle Pleistocene predecessors (Rosenberg et al., 2013; Breeze et al., 2017). Recent research in the Kalahari and Namib Deserts of southern Africa has also highlighted that our species was potentially uniquely able to occupy arid regions during periods of limited surface water in the late Pleistocene (Nash et al., 2016; Dewar and Stewart, 2016). Future work, and the application of palaeoenvironmental methodologies akin to that developed here, should enable further testing as to whether our species is ecologically unique within the genus Homo.

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APPENDIX





1551).



Figure S2. Boxplots of API, BPI, BAI, PCI, and IRSF for modern and fossil Arabian fauna.

Table S1. Stable carbon and oxygen isotope data of the fossil faunal samples analysed in this study. Not all specimenscan be confidently attributed to a unique individual and, therefore, the data may reflect some interindividual variability.

* Denotes specimens also sampled sequentially.

Sample ID	Tooth sampled	Taxa	δ ¹³ C(‰) (VPDB)	S.D.	δ ¹⁸ O(‰) (VPDB)	S.D.
TAG13147 LVLS ref. quartz pebbles	m3	cf. Oryx sp.	-0.8	0.1	0.1	0.2
TAG13147 LVLS ref. quartz pebbles	m2	cf. Oryx sp.	0.6	0.2	0.1	0.4
TAf13/149*	m3	cf. Oryx sp.	1.7	0.1	1.9	0.4
TAG14 Tr5 Lyr 5 TAG14/978	m3	Bovidae	1.0	0.1	4.7	0.1
TAG14 Tr 6 1551*	M2	Oryx sp.	3.3	0.1	3.5	0.1
TAG14 F. max P3 Tr 6 Sq 9 Layer3 1580	P3	Oryx sp.	0.0	0.1	4.8	0.1
TAG14 Tr 5 928	M3	Oryx sp.	-0.4	0.1	-1.6	0.2
TAG14 Tr1 ExT Layer 5 227	pm4	Bovidae	1.1	0.1	-0.4	0.1
TAG14 942*	m2	Bovidae	0.7	0.0	2.8	0.2
TAG14 Tr6 1570	PM2	Bovidae	-0.3	0.1	4.3	0.1
TAG14 1541*	m3	Oryx sp.	2.7	0.1	2.4	0.1
TAG14 944*	M3	Oryx sp.	1.9	0.1	6.2	0.1
TAG14 Tr 5 Layer 5 938	M2	Oryx sp.	0.7	0.1	1.5	0.1
TAG 14 Trench 5 937	M3	Oryx sp.	0.9	0.1	0.5	0.2
SGS-48-P1-P2	M3	Equid	1.9	0.1	0.7	0.1
SGS-57*	M2	Alcelaphus sp.	1.0	0.0	-3.2	0.1
SGS-NAFUD-180*	m2	Equid	-0.1	0.1	-0.5	0.1
SGS-NAFUD-1094*	m3	Equid	0.7	0.1	-5.6	0.2
SGS-NAFUD-1250	m2	Equid	-0.1	0.1	0.1	0.1
TAG14 301	Μ	P. recki	2.2	0.1	0.0	0.1
TAG14 129	M2	P. recki	2.7	0.1	0.9	0.0

Sample ID	Location	GPS	Year of collection	Tooth sampled	Таха	δ ¹³ C(‰) (VPDB)	S.D.	δ ¹⁸ O(‰) (VPDB)	S.D.
H1	TAG	°43'N, 39°37'E	2013	m3	Equus caballus	-8.9	0.1	-3.6	0.1
H2	TAG	°43'N, 39°37'E	2014	m2	Equus caballus	-9.6	0.1	0.9	0.1
H3	TAG	°43'N, 39°37'E	2014	M3	Equus caballus	-9.2	0.1	1.7	0.1
H4	TAG	°43'N, 39°37'E	2014	m2	Equus caballus	-9.0	0.1	-0.6	0.1
CA5	TAG	°43'N, 39°37'E	2014	m2	Camelus	-7.7	0.1	1.8	0.1
					dromedarius				
CA9	TAG	°43'N, 39°37'E	2014	M3	Camelus	-5.9	0.1	0.4	0.1
					dromedarius				0
OR1	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-1.2	0.1	10.0	0.1
OR2	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-2.5	0.1	8.9	0.1
OR3	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-0.1	0.1	8.1	0.1
OR4	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-2.3	0.1	1.3	0.1
OR5	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-2.7	0.1	8.4	0.1
OR6	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-3.9	0.1	6.2	0.1
OR7*	Mahazat as-Sayd	°15'N, 41°40'E	2016	m3	Oryx leucoryx	-1.8	0.1	8.7	0.1

Table S2. Modern faunal samples analysed for stable carbon and oxygen isotopes in this study. * Denotes specimens also
 sampled sequentially

Table S3. Sequential δ^{13} C and δ^{18} O measurements from fossil *Oryx* sp. (specimens TAG13 149, TAG 14 942, TAG14 944, TAG14 1541, and TAG14 1551) analysed in this study.

Distance from root-	δ ¹³ C (‰) (VPDB)	S.D.	δ ¹⁸ O (‰) (VPDB)	S.D.
enamel				
junction				
TAG13 149 – C	Dryx sp.			
0	1.1	0.1	3.9	0.1
5	1.6	0.1	2.6	0.2
10	2.0	0.1	2.1	0.1
15	1.8	0.1	2.6	0.1
20	2.0	0.1	4.1	0.1
25	1.3	0.1	5.1	0.2
30	0.4	0.1	4.2	0.1
BULK	1.7	0.1	1.9	0.1
<u>TAG14 942 – C</u>	<u>)ryx sp.</u>			
0	-0.6	0.1	2.1	0.1
5	-0.5	0.1	3.4	0.2
10	-0.1	0.1	5.4	0.1
15	0.4	0.1	5.9	0.1
20	0.8	0.1	6.3	0.1
25	1.1	0.1	5.2	0.2
30	1.0	0.1	4.6	0.1
35	0.6	0.1	4.0	0.2
40	0.2	0.1	2.8	0.2
45	0.1	0.1	4.5	0.1
50	-0.2	0.1	4.4	0.2
BULK	0.7	0.1	2.8	0.1
TAG14 944 – C	<i>)ryx</i> sp.			
0	1.3	0.1	0.8	0.1
5	1.2	0.1	3.2	0.2
10	0.9	0.1	6.8	0.1
15	0.5	0.1	6.5	0.1
20	0.5	0.1	6.1	0.1
25	0.9	0.1	6.8	0.2
30	1.5	0.1	5.7	0.1
35	1.6	0.1	3.6	0.1
40	1.9	0.1	2.4	0.1
45	2.0	0.1	2.5	0.1
50	1.5	0.1	4.9	0.1
55	2.0	0.1	4.0	0.1
BULK	1.9	0.1	6.2	0.1

Distance	δ ¹³ C (‰)	Standard	δ ¹⁸ O (‰)	Standard
from root-	(VPDB)	deviation	(VPDB)	deviation
enamel				
Junction				
<u>TAG14 1541- C</u>	<u>Dryx sp.</u>			
0	-0.9	0.1	6.5	0.1
5	-0.4	0.1	4.1	0.2
10	0.3	0.1	3.2	0.1
15	1.1	0.1	0.4	0.1
20	1.6	0.1	1.6	0.1
25	2.2	0.1	1.5	0.2
30	2.2	0.1	1.9	0.1
35	2.5	0.1	3.1	0.2
BULK	2.7	0.1	2.4	0.1
<u> TAG14 1551 –</u>	<u>Oryx sp.</u>			
0	1.1	0.1	6.2	0.1
5	1.2	0.1	7.6	0.2
10	2.1	0.1	6.6	0.1
15	2.2	0.1	3.6	0.1
20	2.7	0.1	3.0	0.1
25	2.7	0.1	2.1	0.1
30	2.7	0.1	2.6	0.1
35	2.2	0.1	3.8	0.1
40	1.6	0.1	5.0	0.1
45	1.7	0.1	6.1	0.1
50	1.5	0.1	6.9	0.1
55	1.7	0.1	7.2	0.1
BULK	3.3	0.1	3.5	0.2

Table S3. Continued

Distance	δ ¹³ C (‰)	S.D.	δ ¹⁸ Ο (‰)	S.D.
from root-	(VPDB)		(VPDB)	
enamel				
junction				
<u>SGS 180 – eq</u>	<u>uid sp.</u>			
0	0.8	0.1	1.6	0.1
5	0.7	0.1	2.2	0.1
10	0.7	0.1	0.2	0.1
15	0.8	0.1	2.7	0.1
20	0.7	0.1	3.4	0.1
25	0.9	0.1	4.8	0.1
30	0.7	0.1	3.5	0.1
35	0.5	0.1	2.6	0.1
40	0.7	0.1	2.9	0.1
45	0.5	0.1	2.1	0.1
50	0.5	0.1	1.2	0.1
55	0.3	0.1	1.3	0.1
60	-0.1	0.1	1.2	0.1
65	0.0	0.1	0.8	0.1
70	-0.1	0.1	0.6	0.1
75	-0.4	0.1	-0.9	0.1
80	-0.4	0.1	-1.2	0.1
85	-0.5	0.1	-2.0	0.1
90	-0.3	0.1	-1.9	0.1
BULK	-0.1	0.1	-0.5	0.1
<u>SGS 1094 – е</u>	<u>quid sp.</u>			
0	-0.3	0.1	-3.1	0.1
5	-0.1	0.1	-3.3	0.2
10	0.1	0.1	-3.7	0.1
15	1.1	0.1	-3.3	0.1
20	0.6	0.1	-4.8	0.1
25	0.4	0.1	-5.5	0.2
30	1.1	0.1	-6.8	0.1
BULK	0.7	0.1	-5.6	0.1

Table S4. Sequential δ^{13} C and δ^{18} O measurements from fossil equid sp. (specimens SGS 180, SGS 1094, and SGS 57) analysed in this study.

Distance from root- enamel junction	δ ¹³ C (‰) (VPDB)	S.D.	δ ¹⁸ O (‰) (VPDB)	S.D.	
<u>SGS 57 – Eq</u>	<u>uid sp.</u>				
0	1.6	0.1	-0.3	0.1	
5	1.4	0.1	-0.5	0.2	
10	2.5	0.1	-0.3	0.1	
15	2.4	0.1	-2.4	0.1	
20	2.5	0.1	-2.8	0.1	
25	2.9	0.1	-2.5	0.2	
30	2.6	0.1	-2.5	0.1	
35	2.3	0.1	-3.4	0.1	
40	2.5	0.1	-4.1	0.1	
45	1.0	0.1	-4.6	0.1	
50	-0.1	0.1	-3.1	0.1	
55	-1.9	0.1	-2.4	0.1	
60	-2.9	0.1	-1.5	0.1	
65	-2.9	0.1	-1.5	0.1	
70	-3.0	0.1	-0.5	0.1	
75	-1.2	0.1	-0.5	0.1	
80	-1.9	0.1	-1.0	0.1	
BULK	1.0	0.1	-3.2	0.1	

Table S4. Continued

Distance from root-	δ ¹³ C (‰) (VPDB)	S.D.	δ ¹⁸ O (‰) (VPDB)	S.D.
enamel				
junction				
<u>SGS 301 – Pa</u>	<u>ilaeoloxodon i</u>	<u>reckii</u>	1.0	
0	1.2	0.1	1.6	0.1
5	0.5	0.1	0.0	0.1
10	1.2	0.1	1.0	0.1
15	1.1	0.1	1.2	0.1
20	1.3	0.1	1.6	0.1
25	1.2	0.1	1.0	0.1
30	0.8	0.1	0.7	0.1
35	0.6	0.1	-0.6	0.1
40	0.6	0.1	0.4	0.1
45	0.8	0.1	-0.1	0.1
50	0.8	0.1	1.3	0.1
55	0.6	0.1	1.5	0.1
60	0.8	0.1	1.2	0.1
65	0.5	0.1	0.7	0.1
70	0.9	0.1	0.5	0.1
75	0.6	0.1	-0.6	0.1
80	0.8	0.1	0.4	0.1
85	0.8	0.1	1.1	0.1
90	0.5	0.1	-1.0	0.1
95	1.1	0.1	-0.5	0.2
100	0.6	0.1	-0.5	0.1
105	0.6	0.1	-0.1	0.1
110	0.7	0.1	-0.3	0.1
115	0.4	0.1	-0.7	0.1
120	1.1	0.1	0.5	0.1
125	0.2	0.1	-0.5	0.1
130	-0.1	0.1	-1.0	0.1
135	1.1	0.1	-1.5	0.1
140	0.4	0.1	-2.1	0.1
145	1.2	0.1	-2.5	0.1
BULK	2.2	0.1	0	0.1

Table S5. Sequential δ^{13} C and δ^{18} O measurements from fossil *Palaeoloxodon rechi* (specimenes SCS 301 and SCS 129) analyzed in this study.

Distance from root- enamel junction	δ ¹³ C (‰) (VPDB)	S.D.	δ ¹⁸ Ο (‰) (VPDB)	S.D.
SGS 129 - Pa	laeoloxodon	reckii		
0	5.2	0.1	-1.1	0.1
5	5.1	0.1	-2.3	0.2
10	5.1	0.1	-3.2	0.1
15	4.1	0.1	-3.7	0.1
20	3.9	0.1	-3.1	0.1
25	3.8	0.1	-2.8	0.2
30	3.4	0.1	-0.1	0.1
35	3.4	0.1	0.5	0.1
40	3.8	0.1	-0.1	0.1
45	3.5	0.1	-3.1	0.1
50	3.6	0.1	-3.7	0.1
55	3.3	0.1	-4.2	0.1
BULK	2.7	0.1	0.9	0.1

Table S5. Continued

Table S6. Sequential δ^{13} C and δ^{18} O measurements from modern *Oryx leucoryx* sample (specimen OR7) analysed in this study. Note 1.5‰ has been added to the δ^{13} C values in order to make them comparable to pre-industrial fossil faunal material.

Distance from root- enamel junction	δ ¹³ C (‰) (VPDB	S.D.	δ ¹⁸ O (‰) (VPDB)	S.D.
<u>OR7 – Oryx let</u>	<u>ucoryx</u>			
0	-1.2	0.1	6.7	0.1
5	-0.8	0.1	7.1	0.2
10	0.3	0.1	7.3	0.1
15	-2.0	0.1	6.7	0.1
20	-2.7	0.1	8.1	0.1
25	-0.4	0.1	9.2	0.2
30	-1.3	0.1	9.5	0.1
35	-1.8	0.1	9.9	0.1
BULK	-1.8	0.1	8.7	0.1

Table S7. Results of mixed ANOVA for δ^{18} O by Group (obligate and non-obligate drinker) by Site.

	Degrees of freedom	Sum of squares	Mean square	F value	Pr(>F)*
Group	1	160.6	160.6	43.853	0.000*
Site	3	95.0	31.7	8.643	0.000*
Group:Site	3	100.9	33.6	9.186	0.000*
Residuals	129	472.4	3.7		

*p=<0.05

Table S8. Results of post-Hoc Tukey pairwise comparison for δ^{18} O by Group (obligate and non-obligate drinker) by Site. A= non-obligate drinkers and B= obligate drinkers. Comparisons between A and B are largely meaningless given potential confounding variations in precipitation source, temperature, humidity. As a result the comparisons between non-obligate and obligate drinkers (A and B) for a given site have been highlighted as the most relevant comparisons.

Group	Difference	Lower	Upper	P-value*
B:Laikipia-A:Laikipia	-1.283	-2.957	0.390	0.268
A:Saudi-A:Laikipia	4.158	1.613	6.704	0.000
B:Saudi-A:Laikipia	-3.113	-5.816	-0.410	0.012
A:TAG-A:Laikipia	-1.273	-3.507	0.961	0.650
B:TAG-A:Laikipia	-4.299	-6.844	-1.753	0.000
A:Tsavo-A:Laikipia	-0.763	-3.466	1.940	0.988
B:Tsavo-A:Laikipia	-1.997	-3.478	-0.516	0.001
A:Saudi-B:Laikipia	5.442	2.941	7.943	0.000
B:Saudi-B:Laikipia	-1.830	-4.491	0.832	0.409
A:TAG-B:Laikipia	0.010	-2.172	2.193	1.000
B:TAG-B:Laikipia	-3.015	-5.516	-0.514	0.007
A:Tsavo-B:Laikipia	0.520	-2.141	3.182	0.999
B:Tsavo-B:Laikipia	-0.714	-2.117	0.689	0.769
B:Saudi-A:Saudi	-7.271	-10.552	-3.991	0.000
A:TAG-A:Saudi	-5.431	-8.337	-2.526	0.000
B:TAG-A:Saudi	-8.457	-11.609	-5.305	0.000
A:Tsavo-A:Saudi	-4.921	-8.202	-1.641	0.000
B:Tsavo-A:Saudi	-6.156	-8.533	-3.779	0.000
A:TAG-B:Saudi	1.840	-1.205	4.885	0.579
B:TAG-B:Saudi	-1.186	-4.466	2.095	0.953
A:Tsavo-B:Saudi	2.350	-1.054	5.754	0.403
B:Tsavo-B:Saudi	1.116	-1.429	3.661	0.877
B:TAG-A:TAG	-3.026	-5.932	-0.120	0.035
A:Tsavo-A:TAG	0.510	-2.535	3.555	1.000
B:Tsavo-A:TAG	-0.724	-2.764	1.315	0.957
A:Tsavo-B:TAG	3.536	0.255	6.816	0.025
B:Tsavo-B:TAG	2.301	-0.075	4.678	0.065
B:Tsavo-A:Tsavo	-1.234	-3.779	1.311	0.809

Table S	59. Table	e of the infi	are	d indexes (API, BPI,	BAI, PCI	, WAMPI) for
sample	groups	subjected	to	Fourier-Transform	Infrared	Spectroscopy
diagenes	sis study					

Group	Sample	Taxa	API	BPI	BAI	PCI	WAMPI
Fossil	TAG 14 1551	Oryx sp.	0.06	0.52	8.60	3.84	0.07
Fossil	TAG 14 1541	Oryx sp.	0.08	0.62	7.50	3.68	0.08
Fossil	TAf13/149	cf. Oryx sp.	0.08	0.54	7.00	3.49	0.05
Fossil	TAG14 942	Bovidae	0.17	1.19	7.00	3.55	0.05
Fossil	TAG14 944	Oryx sp.	0.04	0.43	9.50	4.22	0.04
Fossil	SGSNAFUD- 180	Equid	0.10) 0.49 4.9		3.75	0.07
Fossil	SGS-SETA-57	Alcelaphus sp.	0.08	0.38	4.75	4.05	0.06
Fossil	SGSNAFUD- 1250	Equid	0.04	0.49	9.60	3.84	0.04
Fossil	TAG14 301	P. recki	0.03	0.41	9.20	3.92	0.04
Fossil	TAG14 129	P. recki	0.07	0.37	5.29	3.99	0.04
Modern	OR1	Oryx leucoryx	0.23	0.65	3.10	3.30	0.28
Modern	OR2	Oryx leucoryx	0.08	0.47	5.20	3.70	0.11
Modern	OR3	Oryx leucoryx	0.10	0.46	4.60	3.44	0.06
Modern	OR4	Oryx leucoryx	0.07	0.37	5.29	3.54	0.06
Modern	OR5	Oryx leucoryx	0.43	0.92	3.20	2.76	0.34
Modern	OR6	Oryx leucoryx	0.11	0.41	3.73	3.57	0.07
Modern	OR7	Oryx leucoryx	0.08	0.37	4.63	3.58	0.10
Modern	H1	Equus caballus	0.12	0.52	4.33	3.53	0.15
Modern	H2	Equus caballus	0.10	0.43	4.30	3.54	0.06
Modern	H3	Equus caballus	0.14	0.53	3.79	3.46	0.06

Appendix B. Dated Arabian palaeohumidity proxy data

Table S10. Pre-MIS 6 palaeohumidity proxies from Arabia (based on the MIS stage of their mean age). KSA denotes Kingdom of Saudi Arabia, and UAE the United Arab Emirates. In the 'Av.?' column, '+' denotes dates from weighted averaging of statistically coeval dates from deposits bracketing humidity proxies (Drake et al., 2013). Those records existing for northern Arabian are highlighted in orange.

Country	Site	Code	Deposit	Reference	Method	Age (ka)	Range (2σ) (ka)	lσ err.	2σ err.	Av.?	Mean MIS
UAE	Fallaj al- Moalla	RAK/ 00/10/4	Fluvial	Atkinson et al., 2013	OSL	193	131.61- 254.61	31	62		7
OMAN	Wadi Andam/ W. ath Thali	OMF9	Alluvial Fan	Blechschmidt et al., 2009	OSL	194	158- 230	18	36		7
UAE	LIWA	LM-4	Sabkha	Wood et al., 2003	OSL	195	141- 249	27	54		7
OMAN	H13 Hoti Cave	H13 group 6b w. avg.	Speleothem	Fleitmann et al., 2003	UTh	195	190- 220	3	5	+	7
YEMEN	Y99 Al- Mukalla	Y99 group 11 w. avg.	Speleothem	Fleitmann et al., 2003	UTh	207	201- 214	3	6	+	7
KSA	Jebel Qattar		Palaeosol	Petraglia et al., 2012	OSL	211	179- 243	16	32		7
UAE	Buhais	E-72211	Spring	Holzkamper & Mangini, 2008	UTh	212	209- 215	2	3		7
OMAN	Wadi Andam/ W. ath Thai	OMF18	Alluvial fan	Blechschmidt et al., 2009	OSL	213	121- 305	46	92		7
OMAN	W. Adam/ W. Halfayn	OMF5	Alluvial fan	Blechschmidt et al., 2009	OSL	214	176- 252	19	38		7

Country	Site	Code	Deposit	Reference	Method	Age (ka)	Range (2ơ) (ka)	lσ err.	2σ err.	Av.?	Mean MIS
OMAN	Wadi Andam/	OMF15	Alluvial	Blechschmidt	OSL	220	172-	24	48		7
	W. ath Thai		fan	et al., 2009			268				
OMAN	Wadi Andam/ W. ath Thai	OMF10	Alluvial fan	Blechschmidt et al., 2009	OSL	227	173- 281	27	54		7
OMAN	W. Adam/ W. Halfayn Wadi	OMF7&8 w. mean	Alluvial fan	Blechschmidt et al., 2009	OSL	228	221- 235	3	7	+	7
OMAN	Watti Andam/ W. ath Thai	OMF17	Alluvial fan	Blechschmidt et al., 2009	OSL	229	155- 303	37	74		7
YEMEN	Y99 Al- Mukalla	Y97-5 group 9 w. avg.	Speleothem	Fleitmann et al., 2011	Uth	230	222- 239	5	9		7
OMAN	W. Adam/ W. Halfayn	OMF6	Alluvial fan	Blechschmidt et al., 2009	OSL	233	181- 285	26	52		7
UAE	Buhais	E-72177	Spring	Holzkamper & Mangini, 2008	Uth	240	229- 251	6	11		7
YEMEN	Y99 Al- Mukalla	Y99 group 12 w. avg.	Speleothem	Fleitmann et al., 2011	UTh	243	238- 248	3	5	+	8
UAE	Fallaj al- Moalla	RAK/00/20/3	Fluvial	Atkinson et al., 2013	OSL	263	207- 319	28	56		8
UAE	Fallaj al- Moalla	RAK00/20/X	Fluvial	Atkinson et al., 2013	OSL	265	208- 323	29	58		8
UAE	Buhais	E-52925	Spring	Holzkamper & Mangini, 2008	UTh	275	262- 288	7	13		8
YEMEN	Y99 Al- Mukalla	Y99-2 4	Speleothem	Fleitmann et al., 2011	UTh	280	255- 304	12	24		8
YEMEN	Y99 Al- Mukalla	Y99-23	Speleothem	Fleitmann et al., 2011	UTh	292	269- 316	12	23		8

Table S10. Continued.

Table S10. Continued

Country	Site	Code	Deposit	Reference	Method	Age (ka)	Range (2σ) (ka)	1σ err.	2σ err.	Av.?	Mean MIS
KSA	Nefud	(Nefud) 13.5/2	Lacustine	Rosenberg et al., 2013	OSL	293	255- 331	19	38		8
OMAN	H13 Hoti Cave	H13 group 7 w. avg.	Speleothem	Fleitmann et al., 2003	UTh	309	299- 320	5	11	+	9
OMAN	Wadi Andam/W. ath Thali	OMF12	Alluvial fan	Blechschmidt et al., 2009	OSL	317	233- 401	42	84		9
UAE	Fallaj al- Moalla	RAK/00/20/1	Fluvial	Atkinson et al., 2013	OSL	319	262- 377	29	58		9
OMAN	Wadi Andam/W. ath Thali	OMF14	Alluvial fan	Blechschmidt et al., 2009	OSL	323	255- 391	34	68		9
YEMEN	Y99 Al- Mukalla	Y99 group 13 w. avg.	Speleothem	Fleitmann et al., 2003	UTh	328	319- 337	4	9	+	9
UAE	Hafit		Speleothem	Fogg et al., 2002	UTh	337	281- 393	28	56		9
OMAN	Wadi Andam/W. ath Thali	OMF16	Alluvial fan	Blechschmidt et al., 2009	OSL	340	268- 412	36	72		9
OMAN	W. Adam/ W. Halfayn	OMF-5A	Alluvial fan	Juval et al., 1998; Glennie & Singhvi, 2002	OSL	354	240- 468	57	114		9
OMAN	Wadi Andam/W. ath Thali	OMF11	Alluvial fan	Blechschmidt et al., 2009	OSL	407	285- 529	61	112		9
UAE	Buhais	E-72010	Spring	Holzkamper & Mangini, 2008	UTh	410	335- 485	38	75		9
OMAN	Wadi Andam/W. ath Thali	OMF29	Alluvial fan	Blechschmidt et al., 2009	OSL	415	305- 525	55	110		9

Country	Site	Code	Deposit	Reference	Method	Age (ka)	Range (2σ) (ka)	lσ err.	2σ err.	Av.?	Mean MIS
KSA	Ti's al Ghadah	Various	Lacustrine	Stimpson et al. 2015; Rosenberg et al. 2013	Compos.	400	300- 500				11?
KSA	Nefud 16.1	(Nefud) 16.1/2	Lacustrine	Rosenberg et al, 2013	OSL	419	241- 497	39	78		11
OMAN	N Wadi ANdam	OMF28	Alluvial fan	Blechschmidt et al., 2009	OSL	458	264- 652	97	194		12
OMAN	Wadi Andam/W. ath Thali	OMF22	Alluvial fan	Blechschmidt et al., 2009	OSL	621	556- 686	32.5	65		16

Table S10. Continued.

CHAPTER FOUR

Taphonomic and zooarchaeological investigations at the middle Pleistocene site of Ti's al Ghadah, western Nefud Desert, Saudi Arabia

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*The project was conceived and led by MS. MS conduct the taphonomic and taxonomic analysis, IC conducted the diatom analysis, and HSG conducted the lithic analysis. MS prepared the manuscript and all co-authors contributed to the final manuscript.

ABSTRACT

In recent years, the Arabian Peninsula has emerged as a key region for elucidating hominin and faunal evolution and dispersals between Africa and Eurasia. Central to this research is the middle Pleistocene site of Ti's al Ghadah (TAG) which has yielded a diverse and abundant fossil faunal assemblage and the earliest chronometrically dated evidence for hominins in this part of the world. Here, we present the first detailed taphonomic study of the large Unit 5 fossil assemblage from the site. We aim to assess which actor/s were responsible for the accumulation of the assemblage and evaluate evidence that might be consistent with the accumulation of fauna by hominins. We also describe, for the first time, fossils and lithic artefacts from stratigraphic horizons not previously considered, providing taphonomic insights into their accumulation. The taphonomic work shows that the Unit 5 faunal assemblage was accumulated by ambush predators, likely large felids and hominins, in a lake side environment, and that carcasses were subsequently scavenged by more durophagus carnivores such as hyenas and canids. Less can be reliably said regarding the newly described fossil assemblages given their poor preservation and significant wind abrasion, but large carnivores again appear to have played a role, and hominins probably played a role in the accumulation of at least one of these. This study provides the first detail insights into the interplay between hominins, carnivores, and herbivores in Arabia, and suggests that watering holes have been a focus on the Arabian landscape for resources since the middle Pleistocene.
INTRODUCTION

Over the past decade the Arabian Peninsula has seen a dramatic upturn in palaeontological, palaeoenvironmental, and archaeological research (e.g. Parker, 2010; Armitage et al., 2011; Petraglia et al., 2011, 2012; Rosenberg et al., 2011, 2013; Delagnes et al., 2012; Groucutt and Petraglia, 2012; Scerri, 2012; Hilbert et al., 2014; Scerri et al., 2014b, 2015, 2018; Shipton et al., 2014; Breeze et al., 2015, 2016, 2017; Farrant et al., 2015; Groucutt et al., 2015a,b, 2016, 2018; Hoffmann et al., 2015; Jennings et al., 2015; Matter et al., 2015; Parton et al., 2015a, 2015b, 2018; Stimpson et al., 2015, 2016; Guagnin et al., 2018; Roberts et al., 2018). As a result, the significance of Arabia as a stage for African and Eurasian biotic exchanges throughout the Pleistocene and Holocene is increasingly apparent (Chapter Two; Stewart et al., 2017), and it is now evident that hominins dispersed into Arabia by the middle Pleistocene (Groucutt and Petraglia, 2012; Jennings et al., 2015; Scerri et al., 2015; Roberts et al., 2018). This is, however, unsurprising considering the Arabian Peninsula's geographical positioning at the crossroads of Africa and Eurasia, and the episodic increases in precipitation and water availability the peninsula experienced throughout the Pleistocene (Drake et al., 2013; Breeze et al., 2017) that resulted in the establishment of palaeohydrological corridors that linked Arabia to northeast Africa and the Levant (Breeze et al., 2015, 2016; see also Vaks et al., 2007, 2010).

Corresponding influxes of diverse and novel taxa into the Arabian interior, as evidenced by the fossil record, provide further evidence for large-scale increases in water and grassland availability in the region (McClure, 1984; Thomas et al., 1998; Stimpson et al., 2015, 2016; Groucutt et al., 2018). McClure (1984) was the first to report Pleistocene fossils from Arabia following surveys of lacustrine deposits in the Empty Quarter (or Rub' al Khali) that yielded remains of Bos, Bubalus, Gazella, Oyrx, Hippopotamus, and possibly Arabitragus jayakari. Recent excavations at Shi'bat Dihya (SD1) in Yemen (Delagnes et al., 2012) and Al Wusta in northern Saudi Arabia (Groucutt et al., 2018) recovered vertebrate fossil remains in direct stratigraphic association with Middle Palaeolithic artefacts. Significantly, the latter also produced a *H. sapiens* fossil phalanx dated to *c.* 85 ka, as well as fossil fauna consistent with well-watered and vegetated conditions, most notably Hippopotamus (Groucutt et al., 2018). This was further complemented by sedimentary and diatom analysis of the lake marls which indicated relatively shallow and stable freshwater conditions that likely attracted hominins, carnivores, and herbivores (Groucutt et al., 2018). Taphonomic assessment of the fossil assemblage found carnivore tooth marks and breakage patterns suggestive of at least partial accumulation by carnivores, however, the assemblage was too poorly preserved to provide more detailed insights (Groucutt et al., 2018).

Thomas et al. (1998) reported three fossil-bearing lacustrine deposits from the western Nefud Desert. Fossil fauna from these sites, notably alcelaphines, *Palaeoloxodon*, *Pelorovis*, and *Geochelone* sp. cf. *G sulcata*, were argued to reflect past savanna-like conditions in the region, which was further supported by isotopic analysis of fossil fauna teeth that demonstrated an abundance of C_4 grasses in the diets of herbivores (Thomas et al., 1998). Thomas et al. (1998) proposed an early Pleistocene age for the sites based on their interpretation of a mostly extinct fossil faunal assemblage, although more recent radiometric and optically stimulated luminescence (OSL) dating efforts have tied these sites to the pluvial intervals of the middle and late Pleistocene (Rosenberg et al., 2013; Stimpson et al., 2016). Of these three sites, Ti's al Ghadah (locality 2 of Thomas et al., 1998) yielded the largest, best preserved, and most diverse fossil assemblage (see also Stimpson et al., 2015, 2016). Fossils were recovered from a sandy horizon beneath a thick 186 palaeolacustrine deposit and included a relative abundance of *Oryx* fossils, as well as remains of Alcelaphinae, Camelidae, *Vulpes* sp., *Equus* sp., a large osteoglosiform fish, and provisionally identified remains of *Panthera gombaszoegensis* and *Palaeoloxodon recki*.

Stimpson et al. (2015, 2016) provided the first systematic study of Ti's al Ghadah which involved the excavation of six trenches spanning the southern half of the lacustrine exposure and targeting Unit 5 (see their Fig. 3). Combined Electron Spin Resonance (ESR) and U-series dating of fossil teeth, and OSL dating of the fossil-bearing and overlying lake sediments, placed the formation of Unit 5 between c. 500–300 ka, and more likely toward the older end of this range (Rosenberg et al., 2013; Stimpson et al., 2016). Excavations yielded abundant fossil material and increased the faunal diversity of the site. The presence of perennial water and expansive grasslands was further reinforced by the recovery of fossilised remains of fauna with strong affinities for water (Anas, Tachybaptus) and mesowear analysis of elephant molars (Stimpson et al., 2016). The presence of large carnivores (felids, hyenas, and canids) suggested that the western Nefud was host to a substantial prey biomass, and, by inference, a substantial biomass of vegetation (Stimpson et al., 2016). Direct fossil evidence for the presence of large predators (Panthera sp. cf. P. gombaszoegensis, cf. Crocuta crocuta) and scavengers (Neophron percnopterus, cf. varanids), coupled with carnivore tooth-marked bird, equid, and bovid skeletal remains, further suggested that the assemblage was at least in part the result of carnivore accumulation and feeding behaviours (Stimpson et al., 2016). Preliminary taphonomic analysis also found differences in taxonomic representation and preservation between the southern and northern part of the site, although possible processes controlling for these differences were not fully explored.

Cursory investigations of other parts of the basin have reported surface scatters of lithic artefacts and fossil material. Scerri et al. (2015) reported 76 Middle Palaeolithic artefacts from either side of the main palaeolake deposit (region shaded blue in Fig. 1), as well as fossils scattered across the basin. While it is not entirely clear how these relate to the stratigraphy and chronology of the site, given the available dates for the site and the broadly Middle Palaeolithic character of the lithics, they potentially represent the earliest Middle Palaeolithic assemblage in Arabia (Scerri et al., 2015). Stimpson et al. (2016: 16) noted that ephemeral gullies had "eroded fossils from the main lake ridge, re-depositing them unconformably downslope" and reported that older and younger phases of lake formation were preserved within the basin, although their precise stratigraphic positioning was not described.

Renewed investigations of the Unit 5 deposit recovered Middle Palaeolithic artefacts in direct association with the Unit 5 fossils, as well as tentatively identified evidence for the butchery of ungulate remains (Chapter Three; Roberts et al., 2018). Significantly, these findings represent the oldest chronometrically dated hominin presence in Arabia (c. 500-300 ka) and the second Pleistocene site in Arabia demonstrating an unambiguous link between hominins and fossil fauna (Roberts et al., 2018) - the other being the nearby late Pleistocene site of Al Wusta (Groucutt et al., 2018). Stable carbon and oxygen isotope analysis of fossil herbivore teeth from Unit 5 demonstrated productive grasslands and precipitation and humidity levels akin to modern-day East African savannas (Chapter Three; Roberts et al., 2018). Roberts et al. (2018) argued that this, coupled with evidence for hominins at the site, demonstrated that middle Pleistocene hominin dispersals into the Arabian interior required no major novel adaptations. Yet, a key line of evidence for documenting the interactions between hominins, predators, prey, and the environment within Arabia is missing – that is, 188 detailed taphonomic investigations of the fossil assemblages. Here, we present an important step towards addressing this issue by reporting a detailed taphonomic analysis of the well-preserved chronometrically- and stratigraphically-constrained Unit 5 fossil assemblage.

Taphonomic analyses are powerful tools for elucidating the role of biotic and abiotic agents in the accumulation of fossil assemblages (Lyman, 1994). The early recognition that the ways in which hominins and carnivores process carcasses is inextricably tied to feeding behaviour, order of access, and inter- and intra-taxon competition led to a suite of controlled actualistic and naturalistic studies that set out to identify how different bone modifiers may be differentiated from the fossil record (e.g. Blumenschine, 1986, 1988; Marean and Spencer, 1991; Marean et al., 1992; Selvaggio, 1994, Capaldo, 1997, 1998). Such studies demonstrated that the types of prey animals and their ages (e.g. Stiner, 1990; Bunn and Pickering, 2010), skeletal part representation and fragmentation (e.g. Blumenschine, 1986, 1988; Marean and Spencer, 1991; Marean et al., 1992; Faith and Behrensmeyer, 2006; Faith et al., 2007), and the types of bone surface modifications, their location, and frequency (e.g. Blumenschine, 1986, 1988; Capaldo, 1997; Domínguez-Rodrigo, 1999) are reliable indicators of the accumulating agent or agents. For example, it has been repeatedly shown that the damage inflicted on long bone midshafts by hyenas varies greatly depending on whether hyenas have primary or secondary access to carcass parts (Blumenschine, 1988; Capaldo, 1997). Likewise, cut marked long bone midshafts are expected only if hominins had primary access to carcasses or obtained them with substantial scavengable flesh, as is sometimes the case following consumption by large felids (Pobiner, 2007).

This paper has five primary aims:

- (1) We report the results of our geological study of the basin, allowing us to elucidate the relationship between the previously identified but unstudied stratigraphic units, log sections, and sample for diatom analysis in order to gain further insights into the nature of the lacustrine environments in the basin.
- (2) We describe systematically collected fossils and lithic artefacts from stratigraphic horizons not considered previously, providing taphonomic insights into their accumulation. These include taxa identified from new deposits as well as those from recent excavations of Unit 5.
- (3) We conduct inter-trench comparisons with newly collected data to investigate differences in taxonomic representation and preservation between the northern (Trenches 5 and 6) and southern (Trenches 1, 2, and 4) part of the site and explore what this means for the site formation.
- (4) By examining several taphonomic indications, we assess which actor or actors were primarily responsible for the accumulation of the Unit 5 fossil assemblage
- (5) And lastly, we evaluate evidence, outside direct butchery marks, that might be consistent with accumulation of fauna by hominins.

Geographic and geological setting

The site of TAG is situated within an interdunal depression in the southwestern Nefud Desert, approximately 95 km southeast of the city of Tayma, Saudi Arabia (Fig. 1; 27.4330 N, 39.3725 E). The basin lies between two major NW-SE trending traverse barchanoid compound dunes, within which the dominant geomorphological feature is a large NW-SE trending

palaeolake deposit that outcrops over 630 meters and rises to 6 m above the basin floor (Fig. 1). Renewed investigations at the site in 2017 extended the stratigraphic sequence to 10 meters below the modern-day surface of the main palaeolake and recognised three additional fossiliferous and artefact-bearing deposits (Figs. 1 and 2). Although the stratigraphy used in this study closely follows that of Stimpson et al (2015, 2016), our research suggests greater depth and complexity. The following summarises the sequence, and highlights modifications to the previously described stratigraphy.

We recorded a ~50 cm thick iron-rich lake marl deposit occurring at the base of the section (here referred to as Iron Lake; IL), that can be further subdivided into laminated (IL A) and massive (IL B) marls. While IL is clearly a distinct unit from the under- and overlying Unit 1 aeolian sands, it is referred to as "IL" and not "Unit 2" to maintain stratigraphic consistency between previous studies (i.e. Stimpson et al., 2016) and this one. The two lowermost fossiliferous levels occur directly beneath and atop the IL deposit. The most basal of these is a sandstone ridge ($\sim 2500 \text{ m}^2$) situated between the main palaeolake deposit to the east and the large barchan dune to the west (here referred to as the Ti's al Ghadah Sandstone Ridge; TSR). The ridge, which comprises sandstone capped by small in situ fragmentary deposits of IL A, declines westward and is eventually overlain by modern sands. Fossils were recovered from atop and eroding out of this ridge and in some instances fossils retained sandstone cemented to their surfaces, while some lithic artefacts were also recovered as surface finds. Small channels draining from the main palaeolake sequence have eroded and redeposited fossil material downward and westward so that mixing of distinct fossil deposits has occurred, as previously reported by Stimpson et al. (2016). Nevertheless, the fossils from these stratigraphic units appear to be easily distinguishable based on differences in preservation and appearance, such as the presence of cemented sandstone and lighter colour/patina for the TSR fossils.

The second fossiliferous and artefact-bearing level was located just north of TSR and situated stratigraphically above (here referred to as Ti's al Ghadah Iron Lake; TIL). The fossils were found atop the IL B marl (~8000 m²) and the similar sedimentary characteristics between IL A and IL B suggest that they may be laterally continuous with each other and part of the same deposit. Fossils were poorly preserved and share the colour characteristics of the marl suggesting that they are eroded from it. We hypothesize that the TSR and TIL fossils that sandwich the ferruginous marls (IL A and IL B) relate to the expansion and contraction of the lake – that is, the TSR fossils were deposited prior to the lake expanding, whereas the TIL fossils were deposited following the lakes contraction. The Unit 1 aeolian sands extend stratigraphically another 6.5 meters above the TIL deposit, indicating a period of increase aridity and dune mobility.

The greatest sedimentary complexity occurs in the top 2.5 meters of the sequence. The basal two meters are characterised by a succession of cross/horizontally-bedded, pebbly greenish sands that contain abundant root traces (Units 2–5). These are interpreted as reflecting deposition within more humid conditions in association with sheet/surface-wash processes at the margin of the lake basin. This is evidenced by the bedding structures and the presence of pebble sized-clasts. The root traces indicate the presence of vegetation cover that episodically stabilised the land surface, while the greenish sands are interpreted as reflecting elevated groundwater levels and the existence of anoxic conditions. It is within the Unit 5 sands that the major fossil deposit was found, as reported by Thomas et al. (1998) and Stimpson et al. (2015, 2016).

The development of a more extensive lake body is indicated by Units 6–9 which record well-developed marl beds; however, the presence of gypsum crystals, sand beds, and tepee structures indicate that the lake underwent regular drying and desiccation. The stratigraphically youngest fossil bed lies on and within the uppermost section of Unit 9 (~21000 m²) which comprises a series of interbedded sands and gypsiferous marks incised with desiccation cracks that formed during the lake's final desiccation event (here referred to as Ti's al Ghadah Lake Surface; TLS). Progressively thicker palaeolake sediments moving southward suggest that the lake depocenter laid somewhere to the south of the current palaeolake exposure but has since been eroded. Fragmentary fossils and lithic artefacts were found scattered across the surface of the deposit with the greatest concentration occurred towards the southern end of the palaeolake exposure. Some in situ fossils (that is, those found within the Unit 9 sediments) were recovered around its north-western margins. The provenance of the majority of the TLS fossils is uncertain due to most being surface finds, although the few *in situ* fossils recovered from the marl strongly suggest the original depositional context was part of the uppermost unit, with similar states of preservation and appearance suggestive of a single provenance. Nevertheless, the possibility that some of these fossils originated in a discrete but eroded layer that was above the current capping unit cannot be discounted. We hypothesize that the Unit 5 and TLS fossil beds that sandwich the lacustrine marls (Units 6-9) are related to the expansion and contraction of a second younger lake.



Figure 1. Location and stratigraphy of the Ti's al Ghadah site (TAG). A) Red triangle marks the location of Ti's al Ghadah within the western Nefud Desert, Saudi Arabia. B) Oblique 3D view of the topography of the site (derived using a differential GPS), with key landscape units discussed in the text marked.



Figure 2. Stratigraphic log of Ti's al Ghadah showing the sedimentology of exposed marls and sands at the site. The numbering of units follows that of Stimpson et al. (2016) where full descriptions of the sedimentology can be found. Additional units added here are the IL A and IL B ferruginous marls (discussed in text).

METHODS

Diatom analysis

Nine samples for diatom analysis were taken from the ILA, ILB, and Unit 6 diatomaceous marls at a 5 cm spacing. Different methods for diatom analyses were used to produce optimal results due to the low abundance and poor preservation of the diatoms. The standard methods (Renberg et al., 1990) include heating pre-weighed samples in 5ml of 30% hydrogen perioxide (H_2O_2) in test tubes at 90°C until the organic material had been digested, which may take up to two days. Once the tubes had cooled a few drops of 5% hydrochloric acid (HCl) were added to each test tube to remove any remaining carbonates prior to filling the tube with distilled water. The test tubes were settled overnight at 4°C before rinsing the next day. This process was repeated for four consecutive days to ensure samples were clean for slide preparation. A known volume of microspheres was added to the supernatant after the last rinse prior to adjust for the low and high concentrations of each slide (Battarbee and Kneen, 1982). Slides were air-dried at room temperature in a dust free environment for one to two days before mounting with Naphrax diatom mountant. A pilot study was undertaken to find an appropriate concentration and also an alternative method for diatom analysis in attempt to improve the low yield. Following earlier studies (Stoermer et al., 1995; Owen, 2010), the method using HCl was adapted by increasing the concentration of HCl from 10% to 30% and pre-soaking samples to increase the removal of carbonates and ensure cleaner slides which produced similar abundances to the standard methods confirming the low abundances and poor preservation of algae. Diatom taxa were plotted as percentage abundance and the resulting diatom diagrams zoned on the basis of the weighted average distribution of each taxon (Fig. S1 and S2). Both TIL and Unit 6 deposits

contained a relatively low abundance of diatoms and the resulting interpretations should be considered with caution.

Fossil recovery and identification

Excavations of the Unit 5 fossil-bearing layer by the Palaeodeserts Project and the Saudi Geological Survey (SGS) between 2013 and 2017 have produced now 2001 fossil faunal remains that include birds, reptiles, and mammals (see Stimpson et al., 2015, 2016), as well as lithic artefacts (Chapter Two; Roberts et al., 2018). All fossils recovered from Unit 5 have been examined, although not all were included in the present analysis. Fossils recovered during unscreened excavations by the SGS of the Elephant Quarry (n=329), a trench located at the southern part of the palaeolake deposit, were excluded from the main taphonomic analysis but are nonetheless discussed in some detail where we believe this to be informative. The remaining fossil material (n=1672) was recovered during excavation of six trenches targeting Unit 5 by the Palaeodeserts Project between 2013 and 2014. As noted by Stimpson et al. (2016, p. 32), all fossils were recovered from a "discrete unit with little evidence of significant reworking or redeposition", and, therefore, we treat the Unit 5 fossil assemblage as having undergone limited time-averaging. The trenches are in close proximity to one another with the trenches within the southern and northern part of the site being separated by only 10's of meters, while the two regions are only separated by ~ 200 meters. Given the tight stratigraphic association of the fossils, and proximity of the trenches, we treat the entire Unit 5 deposit as a discrete fossil assemblage. All excavated sediment was dry screened using 2 mm mesh sieves, and the locations of diagnostic specimens >5 mm in maximum dimension were recorded by total station (Stimpson et al., 2016). Twentyeight specimens were excluded from the final dataset due to insufficient data collection information and we consider the remaining fossil assemblage to be the Number of Recovered Specimens (NRSP=1644) for analytical purposes. Taphonomic winnowing of unidentifiable fragments <20 mm in maximum dimension (n=1042) further reduced the assemblage that can be analysed, and we refer the remaining fossils to the Number of Identified Specimens (NISP=602). No winnowing based on cortical preservation was conducted, but we note that overall the fossils are well-preserved and exhibited minimal abrasion and cortical exfoliation. A small portion of identified fossils (n=60)were recovered from Unit 5 but no further information regarding which of the trenches they came from was recorded. These fossils were included in the analysis but were excluded from inter-trench comparisons. Thomas et al. (1998) also collected fossils from what is believed to be Unit 5, and although the material they collected was examined by one of us (MS), where each fossil originated from of the three locations reported in their paper is not possible to discern, and, therefore, we have not included their material in the present study.

Pedestrian line surveys of the TSR, TIL, and TLS palaeolake deposits were conducted during the 2017 field season. Surveys were conducted by eight to ten people walking together in a straight line and separated by no more than three meters. The entire exposure of each palaeolake deposit was examined and all fossils collected, and their positions recorded by differential global positioning system (DGPS). When fossils (or lithic artefacts) were discovered, the group halted while fossil location was recorded, specimen numbered, and bagged. Any fossils found eroding out of the palaeolake sediments were carefully removed using trowels. The NRSP for the TSR, TIL, and TSR assemblages are 848, 14, and 801, respectively. Taphonomic winnowing of small and unidentifiable fragments produced an analytical assemblage (NISP) of 622, 5, and 441, respectively. Fossils deemed to have been redeposited downslope from atop the main palaeolake deposit (n=212) were excluded from the analysis.

Fossil identification and analysis was conducted at the Australian National University (ANU) and the University of New South Wales (UNSW), Australia. Each fossil specimen was identified to the lowest taxonomic level possible and facilitated by comparisons with osteological collections housed at the abovementioned institutes and indirect comparisons (photographs, measurements) with material housed at the Smithsonian National Museum of Natural History (NMNH), USA. Specimen morphometric data (length, breadth) was obtained using digital callipers and additional morphometric measures taken following von den Driesch (1976). The key taphonomic principals considered in this study (skeletal part representation, animal size classes, bone fragmentation, bone surface modifications, and mortality profiles) are described below. All fossils are now stored at the Saudi Commission for Tourism and National Heritage headquarters in Riyadh, Saudi Arabia.

Taphonomic analysis

Quantitative units

Results were described using four standard quantitative units: NRSP, NISP, Minimum Number of Elements (MNE); and Minimum Number of Individuals (MNI) (see Lyman, 1994 for a detailed discussion on these quantitative units). MNE was calculated as the minimum number of skeletal units – whole elements (e.g. humerus) or part thereof (e.g. distal humerus) – needed to account for all specimens of a given skeletal unit without taking into consideration the age or side of the animal (Bunn and Kroll, 1986). MNI values were determined similarly to MNE but taking into consideration the age (based on tooth wear, epiphyseal fusion, and bone texture in the case of neonates) and side (for bilaterally paired elements) of the animal. Quantitative units were also normalised (%NISP, %MNE) by dividing all values by the greatest value and multiplying by one hundred (Binford, 1984) to aid in inter-site and inter-study comparisons of skeletal part representation.

<u>Animal size class</u>

Specimens were assigned a size category corresponding to the five sizeclasses described in Bunn (1982), where small, medium, and large denote size classes I-II (< 100 kg; e.g. foxes, gazelle), III-IV (100 kg – 340 kg; e.g. wild asses, oryx), and V-VI (> 340 kg; e.g. hippos, elephant), respectively. The small animal size class includes microfauna (reptiles, birds, rodents), carnivores, and small ungulates, and these groups are often considered separately throughout the present study to highlight differences in the treatment and preservation of these groups.

Bone fragmentation, breakage, and completeness

The analysis of post-depositional fragmentation can provide important insights into the timing and agent of the accumulation of fossil assemblages and represents an important initial step in any taphonomic analysis as skeletal part representation and bone surface modification frequencies are likely to be impacted by the degree of fragmentation. The most basic of these is specimen maximum dimension (or length) which is reported in 10 mm bins up to 100 mm. Two fragmentation ratios based on fossil identifiability are also reported: NRSP/NISP and NISP/MNE for investigating inter-trench and size-biased differences in fragmentation, respectively (see Cannon, 2003). The former is less sensitive to increasing fragmentation than other fragmentation indices, but as it is based on NRSP it cannot be used to investigate taxon- or size-specific differences in fragmentation (Cannon, 2003); for this, we use the second ratio.

Long bone circumference completeness (%) was recorded using the three categories described in Bunn (1982): less than half (Type 1), more than half but not complete (Type 2), and complete (Type 3). During carcass processing and consumption, hominins and large bone-crushing carnivores systematically break open long bones to exploit marrow and as a result tend to generate assemblages dominated by Type 1 shafts (Bunn, 1982; Marean and Spencer, 1991; Marean et al., 2004). On the other hand, less bonedestructive carnivores such as canids and felids typically produce assemblages that comprise more Type 2 and Type 3 shafts (Sala et al., 2014; Arriaza et al., 2016). Consequently, the relative abundance of fragmented and complete long bone shafts provides a valuable means for investigating the role of hominins and carnivores in the accumulation of fossil assemblages.

As a final measure of fragmentation, we recorded long bone fracture patterns as green or dry based on the criteria described by Villa and Mahieu (1991). Bones broken while green (or 'fresh') typically exhibit obtuse or acute fracture angles, a curved outline, and smooth fracture edge, whereas bones broken while in a dry state produce transverse fractures with jagged and stepped edges (Villa and Mahieu, 1991). Bones were recorded as intermediate if they exhibited traits typical of both green and dry broken bones. It should be noted, however, that this system was developed for human long bones, which differ in structure (e.g. cortical thickness, diaphysis length, etc.) to the bones analysed in this study, and was applied to karstic settings, which differ to the open-air setting of the Ti's al Ghadah site. It should also be clearly stated that specimens were not coded as per the original Villa and Mahieu (1991) study, but instead were interpreted/coded as being "green-fractured", "dry-fractured", or "intermediately-fractured" based on the above listed characteristics, as has been done in other studies of similar open-air fossil assemblages (e.g. Yeshurun et al., 2007, 2011; Yeshurun, 2018).

<u>Skeletal part representation</u>

Skeletal part representation can provide important insights into the differential treatment and transport of bones by hominins, carnivores, and abiotic processes such as fluvial transport and post-burial destruction. The relative proportions of each skeletal part were examined according to NISP and MNE. Moreover, we considered the relative proportions of skeletal elements according to body section: skull (cranium, mandible), axial (vertebrae), forelimb (scapula, humerus, radius, ulna), hindlimb (pelvis, femur, tibia, patella), distal limb (carpals, tarsals, metapodials), and feet (phalanges, sesamoids).

Post-depositional survival of skeletal elements is in large part mediated by the physical properties of bone – most notably density – which differ significantly from one skeletal element to another (Lyman, 1984; Lam et al., 1998, 1999). A common method for assessing the role of post-depositional processes in mediating skeletal part representation is to examine the relationship between skeletal part representation and bone mineral density (e.g. Lyman, 1984, Lam et al., 1998, 1999; Faith and Behrensmeyer, 2006; Faith et al., 2007). For small- and medium-sized ungulates we used bone mineral density values calculated from goat (Lam et al., 1998) and wildebeest (Lam et al., 1999) bones, respectively, and corrected for shape and internal cavities when available (BMD₂).

Interpretations of skeletal part representation are complicated by the fact that most high-density elements are low in economic utility, and most

low-density elements high in economic utility (Lyman, 1994). Consequently, skeletal part profiles suffer from equifinality in that various abiotic (e.g. hydraulic winnowing, post-burial destruction) and biotic (e.g. carnivore processing, trampling, hominin transport) processes may generate fossil assemblages that comprise a similar set of skeletal elements. This issue of equifinality may, however, be overcome by considering the economic utility of skeletal elements present in an assemblage, as well as the frequency and location of bone surface modifications which Domínguez-Rodrigo et al. (2007b) refer to as the "physical attribute" taphonomic approach (see also Bar-Oz and Munro, 2004 and references therein). Given that hominins are evidenced at the site by lithic artefacts and probably butchered bones of medium-sized ungulates (Chapter Three; Roberts et al., 2018), it is important to consider the possibility that homining shaped the Unit 5 fossil assemblage by transporting skeletal elements to or from the site. To do so, we compared the skeletal part survivorship to Metcalfe and Jones' (1988) Standardized Food Utility Index (SFUI) for domestic sheep bones. Faith and Gordon (2007) recommend that "low-survival" elements be removed from such analyses as these are readily destroyed by various taphonomic processes (e.g. weathering, carnivore processing, trampling) and are therefore not well-suited for addressing questions regarding hominin butchery and transport decisions in assemblages variously affected by destructive processes. Accordingly, we compared the skeletal part survivorship and SFUI using low- and highsurvival elements and high-survival elements only (i.e. crania, mandible, humerus, radius, metacarpal, femur, tibia, and metatarsal).

Considering the lacustrine setting within which the fossils were deposited (Rosenberg et al., 2013; Stimpson et al., 2015, 2016), it is worth investigating the possibility that the assemblages have undergone hydraulic winnowing. Bones have different transport potentials in water, governed by their shape and density, and, as a result, assemblages significantly influenced 203 by hydraulic winnowing will be overrepresented by elements with either high (transported component) or low (lag component) transport potentials (Voorhies, 1969; Behrensmeyer, 1975; Dechant Boaz and Behrensmeyer, 1976; Fernández-Jalvo and Andrews, 2003). Fossils were placed into transport groups following Voorhies (1969): Group I, bones that float and are highly susceptible to transport (e.g. vertebrae); Group II, bones that are less susceptible to transport and drag as oppose to float (e.g. limb bones); and Group III, the least susceptible to transport (e.g. mandible). As an additional measure for hydraulic influence we calculated the tooth to vertebrae ratio, with values between 0.44–1.5 indicating limited or no hydraulic influence, and values of 3.12–3.48 indicating strong hydraulic influence (Behrensmeyer, 1975).

Bone surface modifications

Each specimen was examined for surface modifications by eye and hand-lens (10-20x) and under different exposures of light to assist in the identification of fine-scale modifications. Closer inspection of selected bone surface modifications was carried out using a binocular microscope (up to 80x) and Scanning Electron Microscopy (SEM; Hitachi S-3400N) in variablepressure mode (VP-SEM) to capture backscatter (BSE) images of the sample surfaces with specimens mounted on SEM stubs using Leit-C-PlastTM carbonbased removable adhesive. Fossils were inspected for cut marks, hammerstone percussion marks, carnivore and rodent gnawing, trampling marks, abrasion, weathering, root etching, and staining, and the anatomical location of each modification recorded.

Cut marks were defined as linear V-shaped grooves often with accompanying shoulder effect, shoulder flaking, and internal microstriations: shoulder effect was defined as shallow striae associated with and running

parallel to, but not more than 0.2 mm from, the main groove; shoulder flaking refers to flaking dents that occur along all or part of the edge of the main groove; and internal microstriations were defined as shallow striae within the main groove and visible at 40x magnification (Olsen and Shipman, 1988; Fisher, 1995; Domínguez-Rodrigo et al., 2009). Trampling marks were differentiated from cut marks in exhibiting a sinuous trajectory, diverse and intersecting striations, and no or irregular internal microstriations (Olsen and Shipman, 1988; Domínguez-Rodrigo et al., 2009). Hammerstone percussion marks refer to pits, grooves, notches, and isolated patches of microstriations (Blumenschine, 1995). Percussion pits are described as shallow U-shaped indentations. These may macroscopically resemble carnivore tooth pits but differ microscopically by the presence of microstriations occurring within or emanating from the pit as a result hammerstone slippage following contact with the cortical surface (Blumenschine and Selvaggio, 1988). Moreover, percussion pits typically lack the crushing of the cortical surface commonly observed in carnivore tooth pits (Blumenschine, 1995). Percussion notches were defined as broad arcuate breaks in the edge of long bone midshafts with corresponding conchoidal medullary flake scars, whereas those produced by carnivores are typically more circular and narrower (Capaldo and Blumenschine, 1994). Carnivore tooth marks were classified into pits, scores, furrows, and punctures following Binford (1981): pits were defined as shallow U-shaped impressions often with crushing of the cortical bone; scores refer to shallow U-shaped longitudinal grooves in the cortical bone; punctures, which include notches, refer to complete perforations of compact bone; and furrows defined as the removal/gouging of cancellous bone. Carnivore tooth pit and puncture mark maximum length and breadth measures were taken following Domínguez-Rodrigo and Piqueras (2003) and were compared to tooth mark dimensions from the literature (e.g. Domínguez-Rodrigo and Piqueras, 2003; DelaneyRivera et al., 2009; Sala et al., 2013). The frequency, location, and qualities of butchery and tooth marks can provided unique insights into the role of hominins and carnivores in the accumulation of fossil assemblages and we compare the data from the present study to landscape and actualistic studies modelling hominin and carnivore feeding behaviours (e.g. Blumenschine, 1986, 1988, 1995; Marean and Spencer, 1991; Marean et al., 1992; Capaldo, 1997, 1998; Faith and Behrensmeyer, 2006; Faith et al., 2007; Gidna et al., 2014; Sala et al., 2014; Organista et al., 2016).

Rodent gnawing marks were described as parallel chisel-like groves with relatively flat bases (Maguire et al., 1980). Root marks, which are generated by the dissolution of bone tissue by chemicals produced directly or indirectly by plant roots, are defined as U-shaped branched grooves often occurring in dense concentrations (Fernández-Jalvo and Andrews, 2016). Each specimen was assigned a weathering stage ranging from zero to five following Behrensmeyer (1978), where stages zero and five represent unweathered and extensively weathered specimens, respectively.

Mortality profile analysis

Mortality profiles, also known as age-frequency distributions, are powerful tools for inferring hominin and carnivore prey selectively and procurement strategies (Bunn and Pickering, 2010). These are often grouped into three main mortality profile models useful for inferring the mode of death of prey populations: catastrophic/living structure, attritional/U-shaped, and prime-age dominated (Stiner, 1990; Bunn and Pickering, 2010; see also Discamps and Costamagno, 2015 and references therein). Catastrophic/living structure mortality profiles resemble stable living populations (that is, there are fewer individuals in successive age classes) indicating that the mode of death was non-biased with respect to age or physical condition and are typically considered illustrative of non-selective ambush hunting (e.g. lion predation) or catastrophic mass death events (e.g. mass kills, flooding, fire, disease). Attritional/U-shaped mortality profiles comprise more weaker juvenile and old individuals that are typically targeted by social cursorial predators (e.g. cheetahs, African wild dogs), although such profiles may also be generated by disease and malnutrition largely affecting weaker individuals (Delgiudice et al., 2006). In contrast, prime-aged dominated mortality profiles comprise mostly the fittest individuals in a population and are often attributed to selective predation by hominins (Stiner, 1990), but, in some cases, may also arise from natural, non-anthropogenic processes (e.g. Wolverton, 2001; Kahlke and Gaudzinski, 2005; Price, 2008).

Mortality profiles were constructed for medium-sized bovids using mandibular tooth-wear stages and specimens placed into one of five age groups following Bunn and Pickering (2010): (1) young juvenile, light to moderately worn deciduous molars and erupting first and second molars; (2) subadult juveniles, moderate to heavily worn or shed deciduous molars and erupting or erupted permanent premolars and molar; (3) early prime, complete permanent dentition with light to moderate wear and without loss of molar infundibulum; (4) late prime, greater wear and no loss of M_1 mesial infundibulum; (5) old, heavy occlusal wear and loss of mesial and distal molar infundibulum. Taphonomic processes (e.g. carnivore feeding, weathering) are known to disproportionately affect young juvenile remains (Behrensmeyer, 1978; Munson, 2000l Munson and Gerniewicz, 2003) and, as such, mortality profile analyses excluding young juvenile remains were also conducted (following Bunn and Pickering, 2010). Mortality profiles were analysed and graphed using the updated modified triangular graph program of Weaver et al. (2011). This program uses likelihood statistics to generate 95% density contours allowing for statistical comparisons between mortality profiles: if the density contours of two samples do not intersect, they are considered to differ 207 at a level of statistical significance. Mortality profiles were also compared using Chi-squared test, or Fisher's exact test when expected values fell below five. We compared the Unit 5 data to mortality profiles of carnivore hunted medium-sized ungulates, as well as ethnographic (Hadza, Kua) and archaeological mortality data. Despite some within-carnivore species and within-predation strategy (ambush vs. cursorial) differences in mortality data – for example, lions in the Kafue National Park were found to take more prime-aged individual than lions in the Serengeti – when plotted in ternary diagrams, the density contours of individual carnivore species and hunting strategies tend to overlap (Oliver et al., 2019). Therefore, we follow Oliver et al. (2019) in pooling species mortality profile data, as well as ambush (lion, leopard) and cursorial (hyena, wild dog) predators.

Lithic analysis

Lithics were classified and recorded according to the methods outlined previously by Groucutt et al. (2015a,b, 2018) and Scerri et al. (2014a, b). This analysis describes the typological and technological features of the assemblages to allow basic comparison to other assemblages. We recorded raw material type, typological category and basic metrics (length, width and thickness) using digital callipers. These characteristics offer an overview of the lithic assemblages, providing both behavioural and taphonomic information for the site.

Statistical analysis

Chi-squared tests were used to investigate the likelihood of independence between two ordinal or nominal variables when expected counts were greater than or equal to five. When expected counts were below five, we used a Fisher's Exact Test instead. Spearman's Rank Order (r_s) and Pearson's Correlation Coefficients (r) were used to measure the strength of the linear association between two variables. Statistical analyses were carried out in PAST (Hammer et al., 2001) and graphics generated using the ggplot2 package (Wickham, 2016) in RStudio (RStudio Team, 2015).

RESULTS

Diatom analysis

Diatom assemblages were recovered from the ferruginous marls (IL A and IL B) and Unit 6. Although the abundance of diatoms was low (yielding about half what is considered sufficient for a statistically valid dataset) they indicate the existence of freshwater, but typically slightly saline/brackish water bodies at this time (Fig. S1 and S2). In IL B, the dominance of Staurosirella lapponica, in samples with the highest number of identifiable valves, implies alkaline lake conditions, whereas the change from a planktonic assemblage towards the base (Lindavia comensis) to a benthic dominate assemblage towards the top (S. lapponica) implies the water body was shallowing. The brackish nature of this water body is indicated by the presence of a number of salinity tolerant species: Denticula kuetzingii, Navicula cincta, and Nitzschia sigma. In Unit 6, the diatoms suggest a neutral/alkaline lake but less alkaline than TIL. Aulacoseira crassipunctata, for example, prefers freshwater of pH of ~5-6, whereas S. pinnata var. *intercedens* prefers pH of ~6.9–8.2. Unit 6 also appears to be less saline than the ferruginous marls as *N. sigma* is the only brackish tolerant species in the assemblage.

Systematic palaeontology

Below we build on the taxonomic identifications of Thomas et al. (1998) and Stimpson et al. (2015, 2016) by describing novel taxa that were encountered during the taphonomic assessment of the Unit 5 fossil deposit (specimen catalogue prefixes: TAG, SGS), as well as identifiable material from the newly investigated deposits. Poor preservation of the TIL fossils prohibited confident taxonomic identification of any of the specimens, but we note that some clearly belong to a very large animal, probably an elephant or hippo. For a complete taxonomic list, we refer the reader to Table 1.

Class **REPTILIA** Laurenti, 1768 Order **SQUAMATA** Oppel, 1811

Renewed investigation of the Unit 5 fossil deposit recovered vertebrae belonging to at least two, and possibly three, species of Squamata. Osteological nomenclature and description of reptiles follows Hoffstetter and Gasc (1969) and Malnate (1972).

Squamata gen. et sp. indet. 1

A small sacrum (TAG14/9346, Trench 6) consists of two fused vertebrae, with slender pleurapophyses, and foramen sacrale. There appears to be no bifurcation of the pleurapophysis of the second vertebrae and a ventral foramen is absent, features which occur in Gekkonidae, Agamidae, and a few Iguanidae, but are not ubiquitous among all species of these families.

Squamata gen. et sp. indet. 2

A vertebra (TAG14/706, Trench 4) with procoelous centra, wide anteriorly positioned transverse processes, and lack of fracture plane, indicating one of the anterior caudal vertebrae. Lack of paired haemapophyses and a strong ventral sagittal ridge suggest this specimen is neither a varanid or *Uromastyx* sp. (Holmes et al., 2010).

Superfamily COLUBROIDEA Oppel, 1811

Colubroidea gen. et sp. indet.

A vertebra (TAG14/710, Trench 4) with a spheroidal joint articulation of the centrum is clearly that of a snake. The presence of a hypapophysis and pronounced neural spine preclude burrowing snakes (e.g. Uropeltidae, Leptotyphlopidae and Typhlopidae) and indicates one of the precaudal vertebra. An anterior keel leading from the hypapophysis is present but does not reach the cotyle. An anteroventrally directed parapophysial process is present, a feature that occurs mainly in the colubroid snakes, and we assign the Unit 5 specimen to the Colubroidea superfamily accordingly.

Class **MAMMALIA** Linnaeus, 1758 Order **LAGOMORPHA** Brandt, 1855 Family **LEPORIDAE** Fischer de Waldheim, 1817 Leporidae gen. et sp. indet.

Left mandible (TAG14/9373, Trench 1) with M_1 and M_2 in place. Both molars are similar in form, although the M_2 is slightly simpler in its overall outline. Each molar displays deep infolding and the posterior lobe is significantly lower than the anterior. Molar morphology differs little among genera of this family, and *Oryctolagus*, *Lepus*, and *Sylvilagus* all overlap in their cheek teeth dimensions, and, as such, we assign this specimen to family level only.

Order RODENTIA Bowdich, 1821 Rodentia gen. et sp. indet.

A single incisor (TAG14/709, Trench 4) with enamel restricted to the buccal surface is clearly that of a rodent, however it is not possible to identify this specimen further.

Order **PROBOSCIDEA** Illiger, 1811 Family **ELEPHANTIDAE** Linnaeus, 1758 Elephantidae sp.

Various tooth enamel fragments (TLS/75, 5149, 5150) recovered from TLS are consistent with elephantids, but the fragments are small and poorly preserved and little more can be said regarding their taxonomy.

Order PERRISODACTYLA Owen, 1848 Family EQUIDAE Gray, 1821 Equidae gen. et sp. indet.

An equid metapodial fragment and single incisor were recovered from TSR and TIL, respectively, however these are poorly preserved and provide no further taxonomic insight.

Order ARTIODACTYLA Owen, 1848 Family **BOVIDAE** Gray, 1821 Subfamily ALCELAPHINAE Brooke, 1876 Alcelaphinae gen. et sp. indet.

Thomas et al. (1998, p. 149) reported "a few isolated lower and upper molars" belonging to an alcelaphine from Unit 5, as well as the nearby late Pleistocene site of Khall Amayshan, but provided no details regarding their appearance or size. Here we report two additional specimens that we refer to Alcelaphinae: an isolated M² (SGS-NEFUD-57) and right maxilla with M¹,

 M^2 , and M^3 in place (SGS-NEFUD-225). Molars are large and most consistent in size with the living wildebeest: *Connochaetes gnou* and *C. taurinus* (Fig. S3). However, they differ from those of comparative specimens of wildebeest in having simpler infundibula, and most notably so in the second molar. In this regard they more closely resemble the teeth of *Alcelaphus* and the extinct *Rusingoryx* but differ from the latter in having a more complex occlusal pattern and pronounced styles and ribs (see Faith et al., 2011). Given the limited number of specimens and difficulties in distinguishing between likesized alcelaphines, we follow Thomas et al. (1998) in referring the specimens described here to Alcelaphinae.

Subfamily **HIPPOTRAGINAE** Brooke, 1876 Genus **ORYX** de Blainville, 1816 *Oryx* sp.

Two left mandibles (TSR/9007, 9017) are referred to Oryx sp. (Fig. 3). Teeth have a simple occlusal outline, ectostylids on the M₁ and M₂, and simple U-shaped infundibulum that become progressively flatter towards the M₃. Second and third molars exhibit pronounced parastylids and goat-folds, features which are often present in the desert-adapted O. dammah but that are typically more subtle in O. leucoryx, O. beisa, O. gazella, and material from Unit 5 (cf. Stimpson et al., 2016, Fig. 12D). The TSR/9007 specimen is notably large and the length of its M₂ (28.5 mm) and estimated length of its M₃ (38.4 mm) exceeds those of the living species, as well as material from Unit 5 (Fig. S4). Thomas et al. (1998) and Stimpson et al. (2016) suggested, based on tooth and palatine morphology, horn core divergence, and body size estimates derived from long bones, that the Oryx present in the Unit 5 assemblage belonged to a large-bodied extinct form of the Arabian endemic O. leucoryx. Given the differences in morphology and large size of the TSR/9007 specimen, it seems reasonable to suggest that at least one other, even older species of *Oryx* may have inhabited the Arabian Peninsula and is represented in the TSR assemblage. In addition, numerous straight, semi-circular horn core fragments consistent with those of *Oryx* were also recovered from TSR, as well as from TLS.



Figure 3. *Oryx* sp. mandible fossils from TSR: (A) TSR/9017; (B) TSR/9007.

Subfamily ANTILOPINAE Gray, 1821

Antilopinae gen. et sp. indet.

A small, well-preserved bovid sacrum (SGS-NEFUD-55, Elephant Quarry) with a greatest length and breadth measuring 83.2 mm and 61.8 mm, respectively. *Oryx* can be discounted based on size alone, which in living species have greatest breadths ranging from 95–153 mm (n=36; data from Peters et al., 1997). Its size is more consistent with smaller antilopines, and the greatest breadth taken from a single comparative *Gazelle gazella* specimen near matched the specimen presented here (61.7mm, data taken from ref. specimen 100, A. Garrad's personal collection, UCL Institute of Archaeology). A small fragmented bovid proximal metacarpal (TSR/885) with an estimated proximal breadth of ~16–18 mm is also probably that of an antilopine and is also consistent in size with *G. gazella* (18.5–22.8 mm, n=25, data from Horwitz et al., 1990). Given the limited material, we attribute both specimens to the Antilopinae subfamily.

Taxonomic representation

Only a few additional taxa were recognised during the present study: a leporid, rodent, and at least two squamates (see Table 1 for complete taxonomic list). The Unit 5 assemblage has a high taxonomic diversity compared to other Pleistocene sites in the Arabian Peninsula with 15 orders and 19 families. The second most diverse fossil assemblage, for example, is the nearby late Pleistocene site of Al Wusta with 5 orders and 5 families.

The abundance of animals according to NISP, %NISP, and MNI is provided in Table 2 and displayed graphically in Figure 4. Medium-sized bovids are the dominant taxon in the Unit 5 deposit (39.2% of NISP), followed by birds (5.1% of NISP), carnivores (3.3% of NISP), small bovids (2.9% of NISP), elephants (2.8% of NISP), reptiles (2.1% of NISP), equids (1.1% of NISP), rodents and leporids (0.5% of NISP), camelids (0.2% of NISP), and indeterminate mammals of varying sizes (42.8% of NISP). Taxa were similarly represented when substituting NISP for MNE and a comparison of the two measures found them to be statistically indistinguishable ($\chi^2 = 1.38$, p = 0.848). *Oryx* is ten times more abundant than alcelaphines (based on MNI values from the Unit 5 and Elephant Quarry assemblages) and we follow earlier studies (Thomas et al., 1998; Stimpson et al., 2016) in suggesting that the bulk of the medium-sized bovid post-crania is attributable to an unidentified and probably undescribed species of *Oyrx*. There are clear and statistically significant differences in taxonomic representation between the southern and northern trenches ($\chi^2 = 28.94$, p < 0.001). A trench-by-trench breakdown (Fig. 4) found that small animals are more common across all three of the southern trenches: rodents, reptiles, and birds are particularly abundant in trenches 2 and 4, whereas carnivores are best represented in trench 1. Equids and elephants are almost exclusively known from the southern trenches and are notably abundant in the Elephant Quarry fossil collection (equid NISP=13, elephant NISP=114). By contrast, the northern trenches are far less taxonomically rich and are overwhelmingly dominated by medium-sized ungulates, and more specifically bovids.

Class	Order	Family	Taxon	xon Common Name		Unit	TSR
						5	
Actinopterygii							
	Osteoglossiformes			Ray-finned Fish		х	
Aves							
	Podicipediformes	Podicipedidae	<i>Tachybaptus</i> sp.	Grebe		х	
	Anseriformes	Anatidae	Anas sp.	Dabbling duck		Х	
	Accipitriformes	Accipitridae	Milvus sp. cf. M. migrans	cf. Black kite		Х	
			Neophron percnopterus	Egyptian vulture		Х	
	Passeriformes	Motacillidae	Motacilla sp. cf. M. alba	cf. White wagtail		х	
			cf. Motacilla	cf. Wagtail		х	
	Pteroclidiformes	Pteroclididae	Pterocles orientalis	Black-bellied sandgrouse		х	
	Struthioniformes	Struthionidae	Struthio sp.	Ostrich		х	
Reptilia							
	Squamata		gen. et sp. indet. 1	Lizard		Х	
			gen. et sp. indet. 2	Lizard		х	
		Agamidae	Uromastyx sp.	Spiny-tailed lizard		х	
		Colubroidea	gen. et sp. indet.	Snake		х	
	Testudines	Testudinidae	Centrochelys sp. cf. C. sulcata	cf. African spurred		х	
				tortoise			
			gen. et sp. indet.	Tortoise	х		
Mammalia							
	Proboscidea	Elephantidae	Palaeoloxodon sp. cf. P. recki	Straight-tusked elephant		х	
			gen. et sp. indet	Elephant	х		
	Perissodactyla	Equidae	Equus sp. cf. E. hemionus	cf. Onager		х	
			Equus sp.	Horse		Х	
			gen. et sp. indet.	Horse	Х		Х

Table 1. Complete taxonomic list of the Ti's al Ghadah fossil assemblages.

Class	Order	Family	Taxon	Common Name	TLS	Unit 5	TSR
	Artiodactyla	Bovidae	<i>Oryx</i> sp.	Oryx	х	х	х
			Alcelaphinae gen. et sp. indet.	Alcelaphine		х	
			Antilopinae gen. et sp. indet.	Antelope		х	х
		Camelidae	Camelus sp.	Camel		х	
	Carnivora	Felidae	Panthera sp. cf. P. gombaszogensis	European jaguar		х	
		Hyaenidae	cf. Crocuta crocuta	cf. Spotted hyena		х	х
		Canidae	Canis ("anthus") lupaster	African golden wolf		х	
			Canis sp.	Canid		х	
			Vulpes sp. cf. V. vulpes	Red fox		х	
		Mustelidae	Mustelidae sp.	Mustelid		х	
	Lagomorpha	Leporidae	Gen. et sp. indet.	Rabbit/Hare		х	
	Rodentia		Gen. et sp. indet.	Rodent		Х	

Table	2.	Species	representa	tion acc	cording	to	NISP	and	MNI	for	the	Unit	5
and El	leph	ant Qu	arry assem	olages.									

	Unit 5		EQ	Unit 5 + EQ	
	NISP	MNI	NISP	MNI	
Birds					
Neoprhon percnopterus	5	1		1	
Pterocles orientalis	1	1		1	
Struthio sp.	2	1		1	
Tachybaptus sp.	1	1		1	
Milvus sp.	1	1		1	
Anas sp.	1	1		1	
Motacilla sp.	2	1		1	
Indet. birds	18		8		
Total birds	31	7	8	7	
Reptiles					
Squamata	9	2	4	2	
Testudines	4	1	4	1	
Total reptiles	13	3	8	3	
Mammals					
Leporidae	1	1		1	
Rodentia	2	1		1	
cf. Mustelidae	1	1		1	
Vulpes sp	4	1	8	1	
Canis sp	4	1	1	2	
Panthera sp.	3	1		1	
Indet. carnivores	8		10		
Small bovids	18	1	4	1	
Indet. small mammals	47		19		
Total small mammals	88	7	42	8	
Alcelaphinae			2	1	
Oryx sp.	240	7	44	10	
Equus sp.	7	2	13	3	
Indet. medium mammals	115		34		
Total medium mammals	362	9	93	14	
Camelidae	1	1	1	1	
Palaeoloxodon sp. cf. P. recki	17	2	114	4	
Indet. large mammals	3		4		
Total large mammals	21	3	119	5	
Indet. mammals	87		60		
Total	602	29	330	37	



Figure 4. Frequencies (%NISP) of taxonomic representation broken down by assemblage (Unit 5, Elephant Quarry), region (northern trenches, southern trenches), and trenches.
	-	Small-sized	Medium-sized	Large-sized	Indetsized	TOTAL
NRCD						1644
NIGI	-	1			/	1044
NISP		132	361	21	88	602
Weathering						
0	n	30	54	1	9	91
1	n	30	104	2	18	154
2	n	18	104	1	17	140
3	n	5	35	3	5	48
4	n	0	5	0	0	5
5	n	0	0	0	0	0
Breakage						
Green	n	4	35	1	4	43
Dry	n	3	30	1	1	34
Intermediate	n	5	7	1	0	12
Midshaft						
circumference	n	3	25	/	4	32
Type 1	n	3	11	/	0	14
Type 2	n	12	33	/	0	35
Type 3						
Carnivore gnawing	-					-
Total	n	14	86	1	12	113
	%	10.6%	23.8%	4.8%	13.6%	18.7%
Epiphysis	n	4	16	0	0	20
	% of	22.2%	25.8%	0.0%	0.0%	24.4%
Midshaft	n	2	20	0	0	22
	% of	57.1%	23.8%	0.0%	0.0%	21.4%

Table 3. Results of the Unit 5 taphonomic analysis broken down by size class ("% of" values refer to the %NISP for the specific bone portion).

Continued.

		Small-sized animal	Medium-sized animal	Large-sized animal	Indetsized mammal	TOTAL
Probable butchery						
marks	n	0	3	0	0	3
Hammerstone(?)	%	0.0%	0.8%	0.0%	0.0%	0.5%
	n	0	2	0	0	2
Cut mark(?)	%	0.0%	0.6%	0.0%	0.0%	0.3%
Rodent gnawing	n	0	2	0	0	2
	%	0%	0.6%	0%	0.0%	0.3%
Root etching	n	3	17	0	4	24
-	%	2.3%	4.7%	0.0%	4.5%	4.5%
Staining (manganese)	n	0	3	0	0	3
	%	0.0%	0.8%	0.0%	0.0%	0.5%
Abrasion	n	1	7	0	0	8
	%	0.8%	1.9%	0.0%	0%	1.3%

	_	Trench 1	Trench 2	Trench 4	Trench 5	Trench 6	
NRSP		834	169	122	68	275	
NISP		321	42	27	68	95	
Weathering							
0	n	53	10	4	3	11	
1	n	85	6	5	24	20	
2	n	72	8	3	20	26	
3	n	25	2	2	7	11	
4	n	1	0	2	2	0	
5	n	0	0	0	0	0	
Breakage	-	-	-	-	-		
Green	n	20	2	3	6	6	
Dry	n	13	0	0	13	5	
Intermediate	n	5	0	0	1	3	
Midshaft							
circumference	n	12	3	2	5	5	
Type 1	n	7	0	0	3	2	
Type 2	n	19	0	0	17	7	
Type 3							
Carnivore gnawing		-			-	-	
Total	n	49	3	3	27	24	
	%	15.3%	7.1%	11.1%	39.7%	25.7%	
Epiphysis	n	5	0	0	9	5	
	% of	13.9%	0.0%	0.0%	29.0%	55.6%	
Midshaft	n	7	1	0	8	2	
	% of	13.5%	20.0%	0.0%	33.3%	14.3%	

Table 4. Results of the Unit 5 taphonomic analysis broken down by trench ("% of" values refer to the %NISP for the specific bone portion).

		Trench 1	Trench 2	Trench 4	Trench 5	Trench 6	
Probable butchery							
marks	n	3	0	0	0	0	
Hammerstone(?)	%	1.0%	0.0%	0.0%	0.0%	0.0%	
	n	1	0	0	1	0	
Cut mark(?)	%	0.3%	0.0%	0.0%	1.5%	0.0%	
Rodent gnawing	n	1	0	0	1	0	
	%	0.3%	0.0%	0.0%	1.5%	0.0%	
Root etching	n	9	0	0	3	10	
_	%	2.9%	0.0%	0.0%	4.4%	10.5%	
Staining (manganese)	n	2	0	0	1	0	
	%	0.6%	0.0%	0.0%	1.5%	0.0%	
Abrasion	n	4	0	0	2	2	
	%	1.3%	0.0%	0.0%	2.9%	2.1%	

 Table 4. Continued.

Taphonomic analysis

Bone fragmentation, breakage, and completeness

The results of the quantitative analysis of the bone surface modifications and fracture patterns are provided in Tables 3 and 4. The Unit 5 assemblage appears moderately fragmented with just under two thirds (61.9% of NRSP) comprising fragments less than 20 mm in maximum length (Fig. 5). This contrasts to highly fragmented fossil assemblage in which almost all fossils are small unidentifiable fragments (e.g. Clark, 2019). The Elephant Quarry assemblage displays an inverse pattern of specimen size distribution, although this is unsurprising given the lack of screening of this section of the site. Specimens greater than 20 mm in maximum length were more-or-less evenly represented in the Unit 5 assemblage. Large animal fossils less than 100 mm in length were rare, and, as such, it appears that their remains have undergone minimal post-depositional destruction. This is further supported by the recovery of complete fragile skeletal elements (ribs, vertebrae) and the discovery of fossils in semi-articulated positions in the Elephant Quarry. Medium-sized ungulates, too, appear to have undergone only moderate post-depositional destruction as evidenced by one third of their skeletal remains exceeding 100 mm in length. The recovery of many complete fragile bird and reptile remains also attests to the limited post-depositional destruction of the Unit 5 fossil assemblage. Fossils from the northern trenches are slightly less fragmented than those from the southern trenches but the distributions of specimen size are more-or-less alike: specimens less than 20 mm in maximum length make up 68% and 55% of the NRSP in the southern and northern trenches, respectively, while specimens of other length categories make up only a small portion each and are similarly represented.



Figure 5. Distribution of frequencies (%NISP) for each specimen size range broken down by assemblage (Unit 5, Elephant Quarry), region (northern trenches, southern trenches), trenches, and animal size class.

NRSP/NISP Based the ratio. the northern trenches on (NRSP/NISP=2.1) are roughly one third less fragmented than the southern (NRSP/NISP=2.9) trenches. Again, this difference is largely driven by Trench 5 which comprises of entirely identifiable elements (NRSP/NISP=1.0). There is little difference in fragmentation across animal size-classes, but carnivores (NISP/MNE=1.1) are the least fragmented taxa, as would be expected in an assemblage influenced by carnivore processing. As a final means of comparison, we compared medium-sized ungulate fragmentation between the northern and southern trenches on the basis that they are the most abundant and ubiquitous taxa represented in the Unit 5 deposit and should therefore provide the best measure of inter-trench differences in fragmentation. Consistent with the results presented above, medium-sized ungulates are less fragmented in the northern (NISP/MNE=1.2) than southern (NISP/MNE=1.5) part of the site (Table S1).

Table 5. Chi-squared test comparisons of shaft ratio (Type 2 + Type 3:Type 1) for the Unit 5, TSR, TLS, and experimental scenarios modelling carnivore primary and secondary access to carcasses [data from Marean et al. (2004) and Sala et al. (2014)].

	Shaft ratio	Unit 5	TSR	TLS
Unit 5	1.53	_	75.852	159.8
TSR	0.12	75.852	<i>p</i> < 0.001 –	p < 0.001 22.481
TLS	0.12	p < 0.001 159.8	22.481	<i>p</i> < 0.001 –
Hyena-only	0.13	p < 0.001 70.21 p < 0.001	p < 0.001 4.821 p = 0.090	27.661 p < 0.001
Hammerstone-only	0.44	13.794 p < 0.001	60.299 p < 0.001	102.010 p < 0.001
Hammerstone-hyena	0.15	79.433 p < 0.001	8.586, p = 0.014	34.497 p < 0.001
Wolf-only	1.73	0.003 p = 0.958	146.02 p < 0.001	233.37 p < 0.001

The shaft ratio (Type 2 + Type 3:Type 1) for small- and medium-sized animals equals 5.0 and 1.76, respectively. Experimental scenarios modelling hominin and hyena feeding behaviours found that the shaft ratio typically ranged between 0.13–0.44 (Marean et al., 2004; Pickering and Egeland, 2006). Therefore, it appears that if hominins and hyenas modified the Unit 5 assemblage, they did so only marginally. These ratios are, however, more consistent with processing by other less bone destructive carnivores such as lions and wolves (Sala et al., 2014; Arriaza et al., 2016). Indeed, a comparison of medium-sized ungulate carcasses processed by wild and captive wolves and the Unit 5 assemblage found no significant difference in shaft circumference completeness (Table 5). In contrast, the Elephant Quarry assemblage shaft ratio (0.52) is more consistent with assemblages processed by hominins and 227 hyenas. An inter-trench comparison found no differences in shaft circumference completeness between the northern and southern trenches across all taxa and size classes ($\chi^2 = 2.54$, p = 0.281) and for medium-sized ungulates only ($\chi^2 = 1.50$, p = 0.472). A statistically significant difference was found, however, when comparing the shaft circumference completeness of small- and medium-sized animals ($\chi^2 = 6.44$, p = 0.040) indicating lesser fragmentation of the former.

Long bone fracture patterns were considered as a final measure of postdepositional fragmentation. Eighty-eight long bone were assessed based on their fracture angles, outline, and edge characteristics. Of these, fragments displaying characteristics consistent with green fracturing (n=43) were more common than those consistent with dry fracturing (n=34), while a small portion was found to exhibit intermediate characteristics (n=11). Long bone fracturing, therefore, occurred at various stages in the post-depositional history of the Unit 5 fossil assemblage. No statistically significant difference was found when comparing the Unit 5 and Elephant Quarry fracture patterns $(x^2 = 1.53, p = 0.216)$. Green fracturing can in part be attributed to carnivore processing, as evidence by green fractured bones bearing large carnivore tooth marks and notches (n=7), while dry fracturing is likely the combined result of weathering and post-burial destruction. No difference in green and dry fractured bone was found between small- and medium-sized animals (Fisher's Exact Test, p = 1.0). Green fractured bone of medium-sized animals was more common in the southern than northern part of the site, although this difference was found to be insignificant ($\chi^2 = 3.35$, p = 0.067).

<u>Skeletal part representation</u>

Almost all elements of the vertebrate skeleton are represented in the Unit 5 assemblage and a complete skeletal inventory is provided in Table 6.

Elements of the crania, appendicular, and forelimb are most abundant in terms of NISP, but the former and the latter are greatly reduced in terms of MNE (Fig. 6), although a chi-squared comparison of NISP and MNE by body portion found these quantitative units be statistically two to indistinguishable ($\chi^2 = 7.673$, p = 0.175). Non-ungulate taxa, and in particular reptiles, carnivores, and elephant, are best represented by axial elements, whereas birds are well-represented by elements of the forelimb. Ungulates are best represented by the appendicular skeleton, and more specifically small- and medium-sized ungulates by elements of the forelimb and distal limb, respectively. Moreover, a number of medium-sized ungulate limb bones were complete: three radii (50% of MNE), two tibiae (18% of MNE), three metacarpals (33% of MNE), and two metatarsals (25% of MNE). We focus the discussion of skeletal part survivorship on ungulates as they make up the bulk of the Unit 5 assemblage and because there has been much research dedicated to understanding how post-depositional processes affect ungulate skeletal remains.

No correlation was found between small-sized bovid limb bone representation and goat bone mineral density (Table 7). Although the sample size is very small, it is consistent with the abovementioned evidence for limited fragmentation of small animal remains. A significant positive correlation was found when comparing medium-sized bovid limb bone survivorship and wildebeest bone mineral density, indicating that a significant portion of the assemblage has undergone density-mediated attrition. This correlation is underscored by the presence of 39 dense midshaft fragments that could not be confidently attributed to a specific limb bone but that probably belong to medium-sized ungulates. No correlation was found between small- or medium-sized ungulate element survivorship and SFUI (Table 7), suggesting that bone density, rather than economic utility, better explains the observed skeletal part profile in the Unit 5 deposit.

229



Figure 6. Frequencies (%NISP, %MNE) of skeletal part representation by body portion (crania, axial, forelimb, hindlimb, distal limb, and feet).

Element	Roden and r	t, bird, eptile	Carn	ivore	Small	bovid	Mediur	n bovid	Eq	uid	Large (elep	animal hant,	Indet. animal (sml / med / lge /
-	-	-	-	-	-	-	-	-	-	-	can	nel)	indet.)
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP
Cranium	5	2	3	2	4	1	24	11	_	_	_	_	1 / 5 / - / 9
Horn core	_	—	—	—	—	_	7	3	_	_	—	_	_/_/_/
Mandible (one side)	1	1	_	_	1	1	26	14	1	4	2	2	-/3/-/2
Tooth	1	1	6	6	2	2	27	27	_	_	7	1	2 / 1 / - / 6
Atlas	_	_	_	_	_	_	4	4	_	_	_	_	-/1/-/-
Axis	_	_	_	_	_	_	5	5	_	_	_	_	_/_/_/
Cervical vertebrae	1	1	_	_	_	_	8	8	_	_	_	_	-/1/-/1
Thoracic vertebrae	_	_	3	3	_	_	8	8	4	4	3	3	1 / 2 / - / 2
Lumbar vertebrae	_	_	2	2	_	_	3	3	_	_	_	_	-/1/-/1
Caudal vertebrae	_	_	1	1	_	_	_	_	_	_	_	_	-/-/1
Indet. vertebrae	11	11	1	1	_	_	_	_	_	_	1	1	2 / 6 / - / -
Furcula / clavicle	2	2	_	_	_	_	_	_	_	_	_	_	_/_/_/
Rib	2	1	_	_	_	_	22	2	_	_	1	1	15 / 44 / - / 22
Sacrum	2	2	1	1	_	_	3	2	_	_	_	_	2 / 1 / - / 2
Sternum	_	_	_	_	_	_	_	_	_	_	_	_	_/_/_/
Scapula	1	1	_	_	2	2	13	4	_	_	_	_	5/3/-/-
Pelvis	_	_	_	_	_	_	6	3	_	_	1	1	4/-/-/1
Humerus	8	5	_	_	3	2	6	4	_	_	_	_	4/1/-/1
- Complete	_		_		_		_		_		_		_/_/_/
- Prox. ep.	_		_		_		_		_		_		1/-/-/1
- Pox. ep. + shaft	2		_		_		_		_		_		1/-/-/-
- MSHF	1		_		3		2		_		_		1/1/-/-
- Dist. ep. + shaft	3		_		_		3		_		_		_/_/_/
- Dist. ep.	1		_		_		1		_		_		1/-/-/-

Table 6. Unit 5 Skeletal part representation according to NISP and MNE.

Element	Roder and 1	nt, bird, reptile	Carn	ivore	Small	bovid	Mediu	m bovid	Eq	uid	Large a (elepl	animal hant, hall	Indet. animal (sml / med / lge / indet)
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP
Radius	1	1	1	1	1	1	6	5	_	_	_	_	-/1/-/1
- Complete	1		_		_		3		_		_		_/_/_/
- Prox. ep.	_		_		1		1		_		_		_/_/_/
- Pox. ep. + shaft	_		1		_		1		_		_		_/1/_/_
- MSHF	_		_		_		_		_		_		_/_/1
- Dist. ep. + shaft	_		_		_		_		_		_		_/_/_/
- Dist. ep.	_		_		_		1		_		_		_/_/_/
Ulna	1	1	_	_	_	_	7	7	_	_	_	_	-/1/-/2
Metacarpal	_	_	1	1	1	1	11	9	_	_	_	_	_/_/_/
- Complete	_		1		1		3		_		_		_/_/_/
- Prox. ep.	_		_		_		1		_		_		_/_/_/
- Pox. ep. + shaft	_		_		_		5		_		_		_/_/_/
- MSHF	_		_		_		_		_		_		_/_/_/
- Dist. ep. + shaft	_		_		_		2		_		_		_/_/_/
- Dist. ep.	_		_		_		-		_		-		_/_/_/
Femur	2	1	_	_	_	_	-	_	2	1	-	_	2 / 1 / - / 1
- Complete	_		_		_		-		_		-		_/_/_/
- Prox. ep.	_		_		—		_		_		_		2/-/-/1
- Pox. ep. + shaft	-		-		_		-		1		-		_/_/_/_
- MSHF	-		-		_		-		_		-		_/1/_/_
- Dist. ep. + shaft	1		-		_		-		1		-		_/_/_/_
- Dist. ep.	-		-		_		-		_		-		_/_/_/_
Tibia	-	_	-	_	_	—	12	11	_	—	-	-	-/2/-/-
- Complete	-		-		_		2		_		-		_/1/_/_
- Prox. ep.	-		-		_		-		_		-		_/_/_/
- Pox. ep. + shaft	-		_		_		1		_		_		_/_/_/

Taphonomy and zooarchaeology of Ti's al Ghadah

Table 6. Continued.

Element	Roden and r	t, bird, eptile	Carn	ivore	Small	bovid	Mediur	n bovid	Eq	uid	Large (elep	animal bhant, mel)	Indet. animal (sml / med / lge / indet)
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP
- MSHF			_		_				_		_		-/1/-/-
- Dist. ep. + shaft	_		_		_		7		_		_		-/-/-/-
- Dist. ep.	_		_		_		2		_		_		_/_/_/
Patella	_	_	_	_	_	_	1	1	_	_	_	_	-/2/-/-
Astragalus	_	_	_	_	1	1	4	4	1	1	_	_	_/_/_/
Calcaneus	_	_	_	_	_	_	3	3	_	_	_	_	_/_/_/
Carpal / tarsal	_	_	_	_	_	_	7	7	_	_	2	2	1/4/-/-
Metatarsal	1	1	_	_	_	_	9	8	_	_	_	_	_/_/_/
- Complete	1		_		_		2		_		_		_/_/_/
- Prox. ep.	_		_		_		1		_		_		_/_/_/
- Pox. ep. + shaft	_		_		_		5		_		_		_/_/_/
- MSHF	_		_		_		_		_		_		_/_/_/
- Dist. ep. + shaft	_		_		_		1		_		_		_/_/_/
- Dist. ep.	_		_		_		_		_		_		_/_/_/
Indet. metapodial	_	_	_	_	1	1	4	_	_	_	1	1	-/1/-/-
Indet. MSHF	7	_	_	_	_	_	1	_	_	_	_	-	5 / 31 / - / 5
Phalanges													
- Proximal	_	_	1	1	1	1	7	7	_	_	_	-	_/_/_/
- Intermediate	_	_	_	_	_	_	4	4	_	_	_	_	_/_/_/
- Distal	_	_	_	_	1	1	_	_	_	_	_	-	_/_/_/
- Indet.	_	_	_	_	_	_	_	_	_	_	_	-	2/-/-/-
Sesamoid	_	_	_	_	_	_	1	1	_	_	_	-	-/1/-/1
Carapace / plastron	1	1	_	_	_	_	_	_	_	_	_	_	_/_/_/
Unidentified	_	_	_	_	_	-	-	_	_	_	_	_	1 / 1 / 3 / 30
Total	47	33	20	19	18	14	239	165	8	7	18	12	47 / 114 / 3 / 88

Table 6. Continued.

Table 7. Results of Pearson's and Spearman's tests for correlation between Unit 5 small- and medium-sized ungulate skeletal part representation, bone mineral density (BMD), and economic utility (SFUI). Data from Tables S2 and S3.

	Sn	nall-size	d ungula	te	Mee	Medium-sized ungulate				
	Pearson		Spear	rman	Pear	rson	Spearman			
	r	p	r_{s}	p	r	p	r_{s}	p		
Bone mineral density (BMD)	0.283	0.129	0.259	0.167	0.543	0.002	0.592	< 0.001		
SFUI (low- and high- survival)	-0.077	0.707	-0.241	0.236	-0.336	0.094	-0.273	0.178		
SFUI (high-survival only)	-0.573	0.137	-0.652	0.114	-0.673	0.067	-0.491	0.221		

All Voorhies' transport groups are well-represented in the Unit 5 fossil assemblage, suggesting that overall the assemblage has not been significantly influenced by hydraulic sorting (Fig. 7). This is also supported by the tooth to vertebra ratio which falls within the range reported by Behrensmeyer (1975) for limited or no hydraulic sorting. However, a closer inspection of the southern and northern trenches identified clear differences in the representation of easy and difficult to transport elements between the two areas. Figure 7 illustrates that easily transported elements are more common in the southern than the northern part of the site and a chi-squared test found the two areas differed significantly ($\chi^2 = 14.136$, p = 0.007). This is also borne out by the tooth to vertebra ratios (Fig. 7), which also differ significantly between the two areas ($\chi^2 = 16.326$, p < 0.001). This suggests that the southern and northern trenches represent transported and lag deposits, respectively. It seems possible that lake level fluctuations spatially arranged elements in the landscape, which, in this instance, appears to have redeposited easy to transport elements further south.



Figure 7. Voorhies transport groups according the %NISP and tooth to vertebra ratio for the Unit 5, northern, and southern trench assemblages. The limited/no (blue) and strong (red) influence bounds are plotted from data taken from Behrensmeyer (1975).

Bone surface modifications – abiotic modifications

Weathering of the Unit 5 fossils ranged from Behrensmeyer's (1978) stage 0-4 with the bulk of the fossils exhibiting stages 0-2 (Fig. 8). Assuming a semi-arid grassland setting similar to the Amboseli National Park, Kenya, most of the bones in this study would have been exposed for 0-6 years prior to burial, while some were perhaps exposed for more than ten years (Behrensmeyer, 1978, Table 2). It should be noted, however, that weathering rate varies according to environment, and bones deposited in wooded (Tappen, 1994), temperate (Andrews and Armour-Chelu, 1998), and desert (Andrews and Whybrow, 2005) settings have all been found to weather slower than those in semi-arid grasslands (Behrensmeyer, 1978). Physiochemical stresses, such as those associated with repeated wetting and drying and fluctuations in temperature, are also known to accelerate bone degradation and weathering (Behrensmeyer, 1978; Haynes, 1988; Pokines et al., 2018). Nonetheless, the varied weathering pattern observed here is not uncommon in open-air bone assemblages (e.g. Behrensmeyer, 1978; Tappen, 1995; Hutson, 2012), and, in this instance, probably reflects a prolonged accumulation of bones which were variably affected by sub-aerial weathering through time. Stimpson et al. (2016) previously noted that the fossils from the southern part of the site were less weathered than those from the northern part of the site and a statistical analysis incorporating new material supports this assertion ($\chi^2 = 10.512$, p = 0.032). However, this difference disappears when examining medium-sized animals only ($\chi^2 = 8.878$, p = 0.064), and, therefore, it appears that this difference is largely driven by the more abundant small animal remains in the southern trenches. Indeed, it is clear from a visual inspection of weathering stages that small-sized animals are less weathered than medium- and large-sized animals (Fig. 8), while a test for correlation found that fossil size and weathering stage were significantly and positively correlated (r = 0.183, p < 0.001; r_s = 0.249, p < 0.001). More rapid burial of smaller bones, possibly facilitated by lake level fluctuations, probably accounts for the differences in weathering, and similar observations have been made elsewhere (Andrews and Whybrow, 2005). Rodent gnawing, manganese staining, and sedimentary abrasion of the Unit 5 assemblages was negligible. Root etching was occasionally observed indicating the deposition of the bones in vegetated soils.



Figure 8. Weathering stage according to %NISP for the Unit 5, southern, and northern trenches, and broken down by animal size.

Bone surface modifications – biotic modifications

Roberts et al. (2018; *Chapter Three*) reported, in addition to lithic artefacts, medium-sized animal ribs and long bones bearing marks reminiscent of cut and hammerstone percussion marks, suggesting that hominins were likely butchering animals at the site, and a complete list of tooth-marked and probably butchered specimens according to element is provided in Tables S4 and S5. During the present analysis, we identified an 237 additional specimen – an adult elephant rib (SGS-NEFUD-108; Fig. 9G) recovered from the Elephant Quarry – bearing several parallel linear grooves reminiscent of cut marks on its ventral face and similar to those reported by Roberts et al. (2018; *Chapter Three*). The markings are bidirectional and run roughly perpendicular to the long axis of the rib. Two of the markings have a deep V-shaped cross-section and exhibit clear shoulder effect, while the others are more surficial. The presence of these markings on the ventral side of the rib suggests that if they are genuine cut marks that they were produced during evisceration, and similar markings have been found on elephant ribs at other middle Pleistocene zooarchaeological sites (e.g. Áridos 2, Spain; Yravedra et al., 2010).

Carnivore tooth marks were commonly observed (18.3% of NISP) and included pits (n=10), scores (n=17), punctures (n=38), and furrowing of cancellous bone (n=38; Fig. 9A-C). Comparable abundances of tooth-marked bones have been observed in modern landscape assemblages in the Park National des Virunga, Democratic Republic of Congo, an area inhabited by non-migratory ungulates, lions, spotted hyena, and leopards (~15%; Tappen et al., 2007). Higher abundances of tooth-marked bones were observed in the Ngamo Pan, Zimbabwe (~42%; Hutson, 2012), and in mostly lionaccumulated carcasses in the Maasai Mara National Park, Kenya (~42%; Domínguez-Rodrigo, 1999), while similar or higher abundances still are typically encountered in carnivore dens (Pickering, 2002; Kuhn et al., 2010). Examining skeletal elements by body portion revealed that limb bones are most frequently gnawed – in the order of hindlimbs (50.0% of NISP), distal limbs (45.6% of NISP), and forelimbs (31.9% of NISP) – followed by elements of the feet (20.0% of NISP), axial (19.6% of NISP), and lastly the cranium (9.2% of NISP). Ribs, too, are frequently gnawed (29% of NISP), which is unsurprising given that these elements are often damaged/destroyed early in the consumption sequence by carnivores during evisceration (Blumenschine, 1986; Domínguez-Rodrigo, 1999). According to body-size, medium-sized animals are most frequently gnawed, followed by small- and large-sized animals (Table 3).

Carnivore diversity in the Unit 5 fossil assemblage suggests that several species may have played a role in the accumulation of the fossil assemblage (see Table 1). Of these, the large-bodied pantherine (Panthera sp. cf. P. gombaszoegensis) and hyena (cf. Crocuta crocuta) are the only capable hunters of medium- and large-sized prey and likely contributed greatest to the accumulation of bones at the site. Canids typically target smaller and more juvenile prey (Stiner, 1990), but like hyena they are highly destructive of bone and exhibit some degree of osteophagy (Sala et al., 2014), and, therefore, may have also significantly impacted the Unit 5 fossil assemblage. Small carnivores (mustelids, Vulpes) were the likely predators of smaller animals such as birds, reptiles, and rodents, and may have also scavenged from the refuse of larger carnivores. To elucidate the role of carnivores in accumulation of the Unit 5 fossil assemblage, we compared tooth mark frequency to actualistic and landscape studies modelling hominin and carnivore feeding behaviours. We focus the discussion on medium-sized animal limb bones (not including the scapula or pelvis) and limb bone units (epiphyses, midshafts) as damage to these elements has been shown to be highly sensitive to hominin-carnivore-carnivore interactions during carcass processing (e.g. Blumeschine, 1988, 1995; Capaldo, 1997; Faith and Behrensmeyer, 2006; Faith et al., 2007; Gidna et al., 2014).



Figure 9. Examples of bone surface modifications from Unit 5 (A–C, G) and TSR (D-F): (A) Oryx sp. metacarpal (TAG14/917) with large carnivore tooth puncture; (B) Oryx sp. distal tibia (TAG14/917) with large tooth puncture and surficial root etching on it's the shaft; (C) Oryx sp. distal humerus (TAG14/1522) with furrowed distal epiphysis and manganese staining on the its shaft; (D) cortical view of a medium-sized animal midshaft fragment (TSR/763) with curved, smooth, and oblique fracture pattern, large flake scar with accompanying ripple marks, and a single angled V-shaped and slightly curved groove with subtle shoulder effect reminiscent of a cut mark; (E) medium-sized animal midshaft fragment (TSR/unnumbered) with three large and arcuate notches with corresponding negative and cortical flake scars; (F) medium-sized animal midshaft fragment (TSR/7126) with a single arcuate notch with corresponding negative flake scar and impact flake on opposing fracture surface; (G) Palaeoloxodon sp. cf. P. recki rib (SGS-NEFUD-108) with several parallel and straight grooves reminiscent of cut marks. The two grooves on the right are comparatively deep and exhibit clear shoulder effect. Scale bars for A–F and G are 20 mm and 20 cm, respectively.

The number of tooth-marked limb bones falls between experimental scenarios modelling carnivore primary and secondary access to carcasses (Fig. 10): there are fewer tooth-marked limbs bones than observed in assemblages generated by hyenas with primary access to carcasses or secondary access to defleshed but unbroken bones (HI, WBH); more tooth-marked limb bones than observed in experimental settings where hyenas had access to only defleshed and demarrowed bones (HHI, HHII); more tooth-marked limb bones than observed in assemblages generated by lions with primary access carcasses (LI, LII); and more tooth-marked limb bones than in to experimental scenarios modelling hominin secondary access following lion processing (LH). Breaking down limb bones into epiphysis and midshaft portions revealed that the epiphyses are more frequently gnawed than the midshafts. The number of gnawed epiphyses is consistent with primary accumulation by lions, but the number of gnawed midshafts falls outside the range for primary accumulation by lions and is consistent with experimental scenarios modelling hyena secondary access to defleshed and demarrowed bone. In this scenario, midshafts are for the most part ignored by hyenas as they offer little nutritional value once hominins have exploited the within bone nutrients (Blumenschine, 1988; Capaldo, 1997). However, as there is limited evidence to suggest that hominins were processing carcasses on-site, a strict hominin-carnivore model of carcass consumption is not currently supported, although some scavenging from hominin kills may have, in fact, occurred. Breaking down limb bones by element found that the femur is the most gnawed limb bone (100% of NISP), followed by the tibia (77% of NISP), radius (40% of NISP), metapodials (37% of NISP), ulna (33% of NISP), and lastly the humerus (17% of NISP). The hind quarters of ungulates are highly nutritious – because of the large amount of flesh and marrow that they bear - and, as a result, are typically the first and often most intensively processed part of the carcass (Blumenschine, 1986; Organista et al., 2016). Intensive processing or transport of the hind quarter would also explain the near-absence of highly nutritious femoral remains, as well as the scarcity of the proximal, but not distal, tibia. While the scarcity of tooth-marked humeri is difficult to reconcile, the lack of highly nutritious proximal humeri epiphyses can probably be attributed carnivore processing. Moderate damage of the metapodials is consistent with the low nutritional value of these elements. Carnivore damage differed between the southern and northern trenches ($\chi^2 = 21.610$, p < 0.001) with those from the latter being significantly more gnawed (Table 4). This statistical difference remained when considering only medium-sized animals ($\chi^2 = 5.844$, p = 0.015), and, as such, it appears that carnivore processing was more intense in the northern part of the site.

The maximum length and breadth measures for tooth pit and puncture size across all skeletal elements ranged from 2.6–16.3 mm (mean=6.0 mm, n=41) and 1.1–16.3 mm (mean=4.3, n=43), respectively. The average tooth mark dimensions most closely resemble tooth pits produced by large carnivores on limb bone epiphyses and shafts, namely by lions, hyenas, and large canids (Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Sala et al., 2014). Some of the smaller tooth pits may have been produced by smaller carnivores (e.g. *Vulpes*) and gnawing of bird birds can probably be attributed to these smaller carnivores (e.g. Stimpson et al., 2016, Fig. 6E).





hyena secondary access to defleshed and demarrowed bones (HHI, HHII; Blumenschine 1995; Capaldo, 1997); wild lion primary access to small/medium-(LI) and large-sized (LII) animals (Gidna et al., 2014); and hominin secondary access to carcasses following processing by lions (LH; Organista et al., 2016).

Asterix (*) denotes samples that do not include metapodials.

Mortality profile

Mortality profile analysis focuses on medium-sized bovids as the sample size for the other size classes was too small, and we include material collected from the Elephant Quarry (n=4) to boost the sample size. According to the relative abundances of each age class, prime-adults (MNI=8) are most abundant, followed by juveniles (MNI=7, young juveniles MNI=4, subadult

juveniles MNI=3), and lastly old individuals (MNI=3). When plotted, the Unit 5 mortality data falls within the living structure space on the ternary plot (Fig. 11). Plotting the 95% confidence intervals found no differences between mortality profiles of medium-sized ungulates from Unit 5 and those killed by wolf (Canis lupus), hyena (Crocuta crocuta), and lion (Panthera leo), but a significant difference between the African wild dog-killed (Lycaon pictus) wildebeest mortality profile which comprises almost entirely of young juveniles (Fig. 11A). Chi-squared and Fisher's exact tests demonstrate significant differences between the Unit 5 mortality data and those of African wild dog and hyena (Table 8). When plotted, the Unit 5 95% CI overlap with both ambush and cursorial predators, although only just with the latter (Fig 10B), while chi-squared tests found that the Unit 5 differed significantly from cursorial predators only (Table 8). Comparisons with ethnographic observations of modern hunter-gatherer hunts (i.e. Hadza, Kua) and mortality data for various African open-air Pleistocene archaeological sites found no differences (Fig. 11C; Table 8). The Unit 5 assemblage sample size is, however, too small to identify any definitive patterns in mortality – that is, the density contours are large and cross into the attritional structure, living structure, and prime-dominated spaces of the ternary plot. Nonetheless, the mortality profile is most consistent with predation by hominins and some non-hominin carnivores, notably ambush predators (e.g. lion), and may reflect the use of ambush predation strategies at a watering hole. On the face of it, this suggest that there may have been a significant amount of vegetative cover around the lake to facilitate hunting by ambush, although additional palaeoenvironmental and palaeobotanical evidence would be needed to test this hypothesis. The abundance of small fragile animal remains (birds, reptiles, rodents) and number of young-juvenile ungulate remains in the Unit 5 assemblage suggests that a bias against young juveniles was likely minimal. Nevertheless, we conducted the above analyses

excluding young juvenile remains and found results to be broadly similar, although with a greater degree of confidence interval overlap and larger p-values across almost all pairwise comparisons (Fig. 11D–F).

Table 8. Chi-squared and Fisher's exact test results comparing mortality profiles of the Unit 5 fossil assemblage with modern carnivore, ethnographic, and zooarchaeological mortality data.

	Unit 5	Unit 5
	(all juvenile)	(subadult juvenile)
Lion	$\chi^2 = 0.727$	$\chi^2 = 0.657$
	p = 0.695	p = 0.720
Leopard	p = 0.796	p = 0.638
Ambush predators	$\chi^2 = 0.535$	$\chi^2 = 0.394$
	p = 0.765	p = 0.877
Hyena	$\chi^2 = 3.947$	$\chi^2 = 0.006$
	p = 0.139	p = 0.997
African wild dog	p < 0.001	p = 0.695
Cursorial predators	$\chi^2 = 7.595$	$\chi^2 = 0.016$
	p = 0.022	p = 0.992
Wolf	p = 0.225	_
Modern human	p = 0.710	p = 0.795
Klasies River Mouth	$\chi^2 = 1.969$	p = 0.850
	p = 0.374	
Bovid Hill	p = 0.788	-
Kanjera South	p = 0.344	p = 0.443
FLK Zinj	p = 0.582	p = 0.642

* mortality data used in the analysis was taken from various sources: lion (Mitchell et al., 1965; Schaller, 1972; Spinage, 1972); leopard (Mitchell et al., 1965); Hyena (Kruuk, 1972); African wild dog (Mitchell et al., 1965; Schaller, 1972); Wolf (Steele, 2004); modern human (Bunn and Gurtov, 2014); Klasies River Mouth (Bunn and Gurtov, 2014); Bovid Hill (Jenkins et al., 2017); Kanjera South (Oliver et al., 2018); FLK *Zinj* (Oliver et al., 2018).



Figure 11. Ternary graphs comparing the mortality profile for medium-sized at Unit 5 to those killed by various carnivores (A, D), ambush (lions, leopards) and cursorial (hyenas, cheetahs, wild dogs) predators (B, E), and data taken from ethnographic and zooarchaeological contexts (C, F). Graphs on the left-hand side (A, B, C) include all individuals, whereas graphs on the right-hand side (D, E, F)

exclude young juveniles. Ellipses approximate 95% confidence (CI) intervals. Shaded regions represent different mortality profile structures as defined by Stiner (1990) and discussed in the text: dark green, juvenile dominated; light green, attritional/U-shaped mortality profile; light brown, catastrophic/living structure; dark brown, prime-age dominated; white, old-age dominated. Sources for mortality data are provided in Table 7.

Initial taphonomic observations of the TAG Sandstone Ridge (TSR), Iron Lake (TIL), and Lake Surface (TLS) fossil assemblages.

Surveys in the TAG basin recovered a wealth of fossiliferous material from two of the three investigated surface deposits: TSR and TLS. The fossil assemblages are poorly preserved and heavily fragmented but differ from one another – notably in their appearance and degree of preservation – suggesting rather distinct taphonomic histories. Very few taxa could be confidently identified (Table 1), and it appears that much of the material is attributable to a medium-sized ungulate. Oryx was the only medium-sized ungulate identified, as represented by numerous mandible and horn core specimens, and, as such, we believe that a significant portion of these assemblages probably belong to this genus. Small-sized animals include at least one other smaller bovid species, as well as tortoise, while elephant was the only largesized animal identified, as represented by a few tooth enamel specimens. We discuss our initial taphonomic observations of each of these assemblages with the caveat that they were collected during pedestrian surveys, and, therefore, are likely biased towards larger, more easy-to-spot fossil specimens, as is implied by the specimen length profiles which comprise few of the smallest fossils (Fig. S5). Moreover, given the surface nature of these deposits, and the mixture of eroded and uneroded materials, it's possible that these assemblages have undergone significant time-averaging. The results of the quantitative taphonomic analysis and complete skeletal part representation of the TSR and TLS assemblages are provided in Tables 9 and 10, respectively.

The shaft ratio for both assemblages is near consistent with those generated by hyena and hominins under experimental settings and most closely matches those produced by hyenas with primary access to carcasses (Table 5). Chi-square test comparisons found no statistical difference between the TSR assemblage and the hyena-only model, while all other comparisons were found to differ significantly. These differences appear largely driven by the greater number of Type 2 and Type 3 long bone midshafts in the experimental datasets when compared to the TSR and TLS assemblages. While carnivore processing may be responsible for the degree of fragmentation in these assemblages, it's possible that abiotic postdepositional destruction processes (e.g. post-burial attrition) also contributed, and the abundant dry-fractured bone in each of the assemblages supports this assertion. Such processes appear to have been more pronounced in the TLS assemblage, as evidenced by the significantly greater number of dry-fractured bone ($\chi^2 = 12.914$, p < 0.001), coupled with the relatively fewer Type 2 and Type 3 long bone midshafts (Table 9) and smaller fossils (Fig. S5). Still, there is an abundance of green-fractured bones in each of these assemblages, attesting to the role of biotic agents in its accumulation and fragmentation, as well as intermediately fractured midshafts, indicating that long bone fragmentation occurred at various points in the history of the deposit. Moreover, it's possible that post-fossilisation processes, such as salt and insolation weathering, have further degraded the fossil assemblages (see also *Chapter Six*). Indeed, much of the fragmentary geological material that fills the western Nefud Desert is thought to be the result of such processes (Edgell, 2006). The role that these processes play in the preservation of coded features (e.g. circumference completeness, fracturing) remains difficult to assess, and, therefore, data on bone fracturing should be interpreted with caution.

The analysis of bone surface modifications was complicated by significant polish, rounding, surficial pitting, and some larger "comet like" pitting consistent with abrasion by fine wind-blown sand (Fig. 12; d'Errico, 1984; Fernandez-Jalvo and Andrews, 2016, Fig. A.119). Although the number of wind-abraded specimens was not precisely recorded, we note that the clear majority of fossils exhibited some degree of polish and/or rounding (e.g. Fig. 9F). Therefore, any reading of the bone surface modifications of the assemblages should bear in mind that wind abrasion has likely obscured or removed much of the bone surface information. Nevertheless, it is possible to make some preliminary inferences regarding the taphonomic history of these assemblages from the bone surface modification data at hand.



Figure 12. SEM images of the cortical surfaces of fossils from Unit 5 (A–B) and TSR (C–D). Note the more textured surface and pitting resulting from sediment compaction (1) in the Unit 5 fossils compared to the polished surface, surficial pitting, and some "comet like" pitting (2) in the TSR fossils resulting from wind and sand abrasion.

The weathering profiles, which include unweathered and extensively weathered fossils, indicate that while some bones were buried rather rapidly, others were likely exposed for some time. Again, this likely represents a prolonged accumulation of bones variably affected by weathering in an openair setting. The two weathering profiles were found to differ significantly (χ^2 = 15.06, p = 0.01) with relatively more stage 3 and stage 4 bones present in the TLS assemblage. The physiochemical stresses associated with weathering degrade bone and promote fragmentation (Hutson, 2018) and the more severe weathering of the TLS fossils would help to explain the relatively greater number of highly fragmented long bone midshafts and dry-fractured bones. No evidence of root etching, rodent gnawing, or staining, and very little evidence for sedimentary/trampling abrasion was observed.

Carnivore tooth-marked bone and hyena coprolites suggest that carnivores played at least some role in the accumulation of the assemblage, consistent with the degree of long bone fracturing and abundance of greenfractured bone. Also, there is tentative evidence to suggest that hominins, too, may have played a role in the accumulation and modification of the TSR assemblage: a medium-sized animal midshaft fragment with curved, smooth, and oblique fracture pattern, large flake scar with ripple marks, and a single angled V-shaped and slightly curved groove with subtle shoulder effect reminiscent of a cut mark (Fig. 9D); two medium-sized animal and one largesized animal midshaft fragments with large arcuate notches with corresponding medullary conchoidal flake scars are most consistent with those generated by hammerstone percussion (Fig. 9E–F); one of these midshafts has two notches with corresponding cortical flake scars (Fig. 9E); while another has an impact scar on the fracture surface opposite the negative flake scar suggestive of breakage and use of an anvil (Fig. 9F). **Table 9.** Results of the taphonomic analysis of the TSR and TLS assemblages

		TSR	TLS
NRSP		848	801
NISP	-	622	441
Weathering			
0	n	79	56
1	n	76	68
2	n	157	124
3	n	81	112
4	n	2	6
5	n	1	0
Indet.	n	226	77
Breakage	-	-	
Green	n	138	70
Dry	n	97	102
Intermediate	n	60	39
Midshaft circumference	-	-	
Type 1	n	290	314
Type 2	n	27	4
Type 3	n	7	1
Carnivore gnawing			
Total	n	33	28
	%	5.3%	6.3%
Epiphysis	n	2	5
	% of	8.7%	16.1%
Midshaft	n	22	19
	% of	5.1%	5.7%
Probable butchery marks	•	-	-
Hammerstone(?)	n	3	0
	%	0.4%	0.0%
Cut mark(?)	n	1	0
	%	0.2%	0.0%
Rodent gnawing	n	0	0
	%	0.0%	0.0%
Root etching	n	0	0
8	%	0.0%	0.0%
Staining	n	0	0
(manganese)	%	0.0%	0.0%
Sediment/trampling abrasion	n	4	4
ping astasion	%	0.6%	0.9%
Covered in sediment	n	29	0
colorou in southont	%	4.7%	0.0%

("% of" values refer to the %NISP for the specific bone portion).

Element	TSR	TLS	
	NISP	NISP	
	(sml/med/lge/indet.)	(sml/med/lge/indet.)	
Cranium	1/19/-/11	-/2/-/6	
Horn core (one side)	-/27/-/-	-/5/-/-	
Mandible (one side)	-/24/-/1	2/2/-/3	
Tooth	3 / 16 / – / 1	-/13/3/-	
Atlas	-/1/-/1	_/_/_/_	
Axis	-/1/-/-	_/_/_/_	
Cervical vertebrae	1/5/-/4	2/2/-/-	
Thoracic vertebrae	-/2/-/1	1 / - / - / 1	
Lumbar vertebrae	_/_/_/	_/_/_/_	
Caudal Vertebrae	_/_/_/	_/_/_/_	
Indeterminate vertebrae	-/3/2/5	3 / 5 / - / 10	
Furcula / clavicle	_/_/_/	_/_/_/_	
Rib	3 / 12 / 5 / 13	-/10/3/3	
Sacrum	_/_/_/	_/_/_/_	
Sternum	_/_/_/	_/_/_/_	
Scapula	4 / 7 / - / 2	-/1/-/2	
Pelvis	1/-/-/-	-/1/-/-	
Humerus	-/15/-/-	-/4/-/1	
- Complete	_/_/_/	_/_/_/_	
- Prox. ep.	_/_/_/	_/_/_/_	
- Pox. ep. + shaft	_/_/_/	_/_/_/_	
- MSHF	-/14/-/-	_/3/_/_	
- Dist. ep. + shaft	_/_/_/	_/_/_/_	
- Dist. ep.	-/1/-/-	-/1/-/1	
Radius	-/10/-/1	1 / 7 / - / 1	
- Complete	_/_/_/	_/_/_/_	
- Prox. ep.	-/1/-/-	-/2/-/-	
- Pox. ep. + shaft	-/5/-/-	1/2/-/-	
- MSHF	-/4/-/-	-/2/-/-	
- Dist. ep. + shaft	_/_/_/	_/_/_/	
- Dist. ep.	_/_/_/	-/1/-/1	
Ulna	_/_/_/	-/1/-/1	
Metacarpal	1/-/-/-	-/1/-/-	
- Complete	_/_/_/	_/_/_/	
- Prox. ep.	_/_/_/	-/1/-/-	
- Pox. ep. + shaft	1 / - / - / -	_/_/_/	
- MSHF	_/_/_/	_/_/_/	
- Dist. ep. + shaft	_/_/_/	_/_/_/	
- Dist. ep.	_/_/_/	_/_/_/	
Femur	-/1/-/-	2/-/-/1	
- Complete	_/_/_/	_/_/_/	
- Prox. ep.	-/1/-/-	2/-/-/-	
- Pox. ep. + shaft	_/_/_/	_/_/_/	
- MSHF	_/_/_/	-/-/1	
- Dist. ep. + shaft	_/_/_/	_/_/_/_	
- Dist. ep.	_/_/_/_	_/_/_/	

Table 10. Skeletal part representation for the TSR and TLS assemblagesaccording to NISP.

Element	TSR	TLS	
	NISP	NISP	
	(sml/med/lge/indet.)	(sml/med/lge/indet.)	
Tibia	_/5/_/_		
- Complete	_/_/_/	_/_/_/	
- Prox. ep.	_/_/_/	_/_/_/	
- Pox. ep. + shaft	_/_/_/	_/_/_/	
- MSHF	-/1/-/-	-/2/-/-	
- Dist. ep. + shaft	-/3/-/-	-/2/-/-	
- Dist. ep.	-/1/-/-	_/_/_/	
Patella	_/_/_/	_/_/_/	
Astragalus	-/3/-/-	_/_/_/	
Calcaneus	-/2/-/-	_/_/_/	
Carpal / tarsal	-/1/1/-	-/4/-/2	
Metatarsal	-/4/-/-	1/1/-/-	
- Complete	_/_/_/	_/_/_/	
- Prox. ep.	_/_/_/	1/-/-/-	
- Pox. ep. + shaft	-/4/-/-	-/1/-/-	
- MSHF	_/_/_/	_/_/_/	
- Dist. ep. + shaft	_/_/_/	_/_/_/	
- Dist. ep.	_/_/_/	_/_/_/	
Indet. metapodial	2 / 15 / - / -	3/21/-/-	
Indet. midshaft	20 / 357 / 6 /	24 / 261 / 14 / -	
Phalanges			
- Proximal	-/-/1/-	-/1/-/-	
- Intermediate	_/_/_/	_/_/_/	
- Distal	_/_/_/	-/3/-/-	
Sesamoid	_/_/_/	_/_/_/	
Carapace / plastron	1/-/-/-	2/-/-/-	
Total	37 / 530 / 15 / 40	41 / 349 / 20 / 31	

Table 10. Continued.

Only fourteen fossils were collected from the TIL area; nine of these displayed preservation and colour characteristics similar to that of the TLS fossils and were excluded, leaving five specimens confidently assigned to the TIL deposit. The only two identifiable bones were long bone shaft fragments, and it appears that all specimens are from very large mammals. The fossils exhibit significant exfoliation and exposure of underlying cancellous bone, although they appear to be less rounded than fossils from the other two assemblages. Future systematic excavation of the TIL palaeolake may yield fossiliferous material suitable for detailed zooarchaeological and taphonomic analyses.

Lithic analysis

With the caveat that the new lithics assemblages are small, and those for TIL and TSR are very small, we describe the basic features of the new assemblages. No large cutting tools (e.g. handaxes) have been found in the TAG basin, nor diagnostic debitage associated with their production (e.g. biface thinning flakes). Likewise, diagnostically young features, such as high levels of exotic raw materials and arrowheads, are absent. The overall features of all assemblages are consistent with a Middle Palaeolithic attribution. In total, 156 lithic artefacts were recovered: 12 from TIL, 10 from TSR, and 134 from TLS.

The basic typological features of the assemblages are listed in Table 11. All assemblages are dominated by flakes, which (excluding Levallois flakes) make up between 75 and 63% of the assemblages. Levallois flakes are relatively common. Retouched tools are only present in the TLS assemblage, where they make up a relatively large proportion of the assemblage compared to other Middle Palaeolithic assemblages. Levallois cores are present in the TLS assemblage, but non-Levallois cores are common. Chips and chunks are present in very low frequencies. These technological features suggest a coherent character to hominin behaviour. They indicate the import of lithics to the site, as indicated by high frequencies of Levallois flakes and, in the TLS assemblage, retouched flakes.

Table 11. Basic typological composition of the Ti's al Ghadah lithic assemblages (% are shown in brackets and refer to the % of each category within each assemblage).

Site	Flake	Broken flake	Lev. flake	Retouched	Lev. core	Non-Lev. core	Chips/ chunks
TIL	5 (41.7%)	4 (33.3%)	2 (16.7%)	/	/	/	1 (8.3%)
TSR	7 (70%)	/	1 (10%)	/	/	1 (10%)	1 (10%)
TLS	68 (50.7%)	16 (11.9%)	19 (14.2%)	10 (7.5%)	7 (5.2%)	13 (9.7%)	1 (0.7%)
Unit 5	6 (46.2%)	/	/	1 (7.7%)	/	/	6 (46.2%)

The Levallois flakes and cores present a consistent insight into the character of the reduction process. Striking platforms are generally facetted, and debitage surfaces were prepared centripetally. Both centripetal preferential and recurrent Levallois cores are present. A single exception is a Levallois point/triangular flake with unidirectional convergent preparation from TLS. Non-Levallois cores are either multiplatform or single platform. These may indicate some chronological variation in the samples but are also not inconsistent with a Middle Palaeolithic attribution for all of the material. The retouched artefacts are generally rather basic laterally, and sometimes distally, retouched flakes.

Table 12 summarise the raw material used in the assemblages. The main materials used were different forms of quartzites. This is similar to other sites in the area (Breeze et al., 2017; Groucutt et al., 2017; Groucutt et al., 2018). Ferruginous quartzites are generally found in iron rich horizons within the sandstones in the Nefud region. Other forms of quartzites appear to occur as generally rounded pebbles, of either fluvial or conglomeritic origin.

Our surveys in the area suggest that ferruginous quartzite exposures, which are the key raw material source for most Pleistocene sites in the region (*ibid*), are sparse in the area close to TAG. This may correlate with the frequent use of chert, which is of a poor quality, lacustrine form that is found outcropping locally. The only other site identified in the Nefud where this chert was also used in high frequencies is the site of Al Wusta, three kilometres from TAG, where similar low-quality chert is the most common raw material used (Groucutt et al., 2018). This paucity of good raw material in the area may explain some of the characteristics of the TLS assemblage, where Levallois flakes and retouched tools are present in quite high frequencies. This suggests that these were curated objects, carried into the dune field.

Assemblage	Chert	Ferruginous quartzite	Other quartzite	Quartz	Igneous
TIL	1 (8.3%)	9 (75.0%)	/	/	2 (16.7%)
TSR	3 (30%)	4 (40%)	3 (30%)	/	/
TLS	53 (39.6%)	46 (34.3%)	32 (23.9%)	3 (2.2%)	/
Unit 5	13 (100%)	1	/	/	/

Table 12. Raw material composition of the Ti's al Ghadah lithic assemblages (% are shown in brackets and refer to the % of each category within each assemblage).

Table 13 summarises mean average values for basic metric features of flakes in each assemblage, as a way to offer a basic summary of the size and shape of the TAG lithics. This both highlights the basic similarities between the sizes of flakes in the different assemblages, and also indicates the generally small size of flakes. The small average size of flakes also demonstrates the systematic nature of the survey transects. Small flake size
also suggests that relatively small clasts were being worked, and relatively small artefacts transported to the site. In fact, the TAG flakes are very short for a Middle Palaeolithic assemblage – being shorter than those from Middle Palaeolithic sites such as Tor Faraj, Warwasi (layers WWXX), JKF-1 and Porc Epic (Groucutt, 2014). However, the flakes are on average thicker than in all of these assemblages, and wider than most of them. The knappers at TAG were generally producing relatively thick and squat flakes. The mean average for elongation (length/width) at TAG is 1.3, which is very squat for a Middle Palaeolithic assemblage – flakes at Tor Faraj and Porc Epic have average values of 2.1 and 2, respectively (Groucutt, 2014). These features probably reflect a combination of both raw material and technology.

The newly recovered lithics were found relatively evenly distributed across the surveyed areas, and not in discrete 'knapping scatters'. While their distribution may have been influenced by taphonomic processes, it is also parsimonious that they represent artefacts abandoned during repeated hominin visits to the locality.

Table 13. Comparison of basic flake dimensions for each assemblage, only using complete, unretouched flakes. All measurements in mm. First three columns are for all complete flakes, right hand three columns are only for complete flakes over 20mm, to allow comparability.

Assemblage	Flake mean length	Flake mean thickness	Flake mean width	Flake >20mm mean length	Flake >20mm mean thickness	Flake >20mm mean width
TIL	31.2	12.2	26.4	31.7	12.2	26.4
TSR	43.6	14.3	33.9	48.1	15.9	36.9
TLS	30.6	10.4	28.0	32.6	10.8	28.6
Unit 5	20.1	8.5	13.8	23.9	9.2	14.6

DISCUSSION

Ti's al Ghadah is the most significant Pleistocene palaeontological site in Arabia, and this is further underscored in the current study by the identification of new fossil- and artefact-bearing deposits that relate to temporally discrete phases of lake formation within the Ti's al Ghadah basin. Previous analyses of the Unit 5 fossil deposit have identified a diverse suite of fauna illustrative of semi-arid grassland conditions, evidence for carnivore processing of bone, and the earliest traces of hominin activity in Arabia in the form of lithic artefacts and probably butchered bone (Thomas et al., 1998; Scerri et al., 2015; Stimpson et al., 2015, 2016; Roberts et al., 2018). The current study presents a detailed taphonomic assessment of this site in an effort to determine the main bone accumulation processes and elucidate the relative roles of hominins, carnivores, and environment in the formation of the assemblage. In turn, this provides a unique insight into the palaeoecology of the Arabian Peninsula during middle Pleistocene. The Unit 5 assemblage is well-preserved and appears to have undergone minimal post-depositional destruction, as evidenced by the recovery of complete fragile skeletal elements, abundant small bird, rodent, and reptile remains, limited fragmentation of long bone midshafts, and the discovery of bones in semi-articulated states. The northern part of the site is far less taxonomically rich, and this may relate to the preferential transport of small-sized animal remains driven by lake level fluctuations. Indeed, Rosenberg et al. (2013) noted that the facies associated with the palaeolake sediments overlying Unit 5 were characteristic of a near-shore position within the lake. Preferential transport is also supported by the Voorhies transport group analysis that found easy to transport elements were more concentrated in the southern trenches. If bones were fluvially transported, the lack of evidence for rounding and sediment abrasion suggests that this occurred in a low energy environment consistent with a lake shore.

Carnivores contributed at least partially to the accumulation and modification of the Unit 5 fossil assemblage, as evidenced by tooth-marked and green-fractured bone, and their presence is confirmed by the discovery of carnivore remains and coprolites (Thomas et al., 1998; Stimpson et al., 2015, 2016; Roberts et al., 2018). The skeletal part representation and distribution of carnivore tooth marks is broadly consistent with processing by large carnivores – that is, highly nutritious elements (e.g. ribs, femur, pelvis) are commonly gnawed and highly nutritious element portions (e.g. proximal humerus, proximal femur) are generally underrepresented in relation to less nutritious elements (cf. Blumenschine, 1986; Marean and Spencer, 1991; Marean et al., 1992; Domínguez-Rodrigo, 1999; Faith and Behrensmeyer, 2006; Faith et al., 2007). The number of tooth-marked limb bones falls between experimental models of carnivore primary and secondary access to carcasses following processing by hominins but is near consistent with the latter. However, a strict hammerstone-carnivore model of bone accumulation is at odds with the abundance of Type 3 long bones, as well as the scarcity of even tentatively assigned butchery marks. For example, Capaldo (1997) found that in assemblages first processed by hominins and subsequently scavenged by hyenas that 13–23% and 9–25% of medium-sized animal limb bones retained cut and percussion marks, respectively. Similarly, Blumenschine and Selvaggio (1998) noted in their hammerstone processing experiments that roughly one third of the resulting limb bone fragments bore at least one percussion mark.

Alternatively, the low number of tooth-marked long bones may reflect primary access to carcasses by large felids, which is also supported by the abundance of Type 3 long bones and the living structure mortality profile (although the latter is also consistent with a number of zooarchaeological assemblages). Felids are specialised flesh-eaters with teeth especially designed for meat slicing, and, as a result, generate comparatively fewer tooth marks and broken bones during carcass processing than do more durophagous carnivores like hyenas and canids (Turner and Anton, 1997; Domínguez-Rodrigo et al., 2007; Pobiner, 2007; Gidna et al., 2014; Arriaza et al., 2016; Aramendi et al., 2017). Indeed, the number of tooth-marked epiphyses falls within the range observed in modern landscape assemblages accumulated by wild lions (Fig. 10). The survival of a number of complete long bones and axial elements also points to a large felid as the primary accumulator of bones at the site. The number of tooth-marked midshafts and abundant green-fractured bones is, however, at odds with carcass processing by large felids only and suggests that more durophagous carnivores on occasion scavenged from large felid kills. However, we cannot discount that the large felid identified in the Unit 5 assemblage (Panthera sp. cf. P. gombaszoegensis) had a different feeding behaviour to extant analogues.

Indeed, during the Pleistocene an evolutionary trend in large felids from a "chewing" dentition to one more specialised for "meat-slicing" has been reported, and among the Pleistocene pantherines Panthera gombaszoegensis was particularly well-adapted to bone crushing (Hemmer et al., 2010; Diedrich, 2013). Moreover, jaguars (Panthera onca), which are thought to be closely related to the extinct Panthera gombaszoegensis (Turner and Antón, 1997), have recently been shown to inflict damage to bones that are more comparable with durophagus carnivores such as hyena (Rodríguez-Alba et al., 2019). Nonetheless, the direct fossil evidence for hyenas and canids, significant density-mediated attrition among medium-sized ungulate limb bones, and abundant green-fractured long bones suggest that these carnivores played some role in the modification of the Unit 5 assemblage and similar frequencies of tooth-marked midshafts have been observed in the FLK North 3 and FLK North 4 fossil assemblages (Olduvai Gorge, Tanzania), two sites thought to be accumulated by large felids and intermittently scavenged by hyenas (Domínguez-Rodrigo et al., 2007a). Smaller carnivores such as foxes (*Vulpes* sp.) and mustelids, as well as non-mammalian carnivores such as vultures (Neophron percnopterus) and varanids, may have also scavenged from large carnivore refuse, and are probably responsible for the accumulation of small bird, reptile, and rodent remains at the site. The presence of vultures implies limited or no tree/bush cover (Domínguez-Rodrigo, 2001) and suggests that ambush hunting at the lakeside was probably facilitated by high grasses. Hunting at the site was focused on medium-sized ungulates, most notably oryx and equids. Lions are specialist hunters that preferentially target a narrow range of medium-sized ungulate taxa, whereas hyena are generalist predators that take a wider range of prey/scavenged species (Hayward and Kerley, 2005; Hayward, 2006). The relative abundance of oryx remains at the site is therefore consistent with accumulation by a specialist carcasses collector (e.g. lion). Deaths not due to

carnivore predation may have also provided some input of bones into the landscape.

Hominins may have also engaged in scavenging at Unit 5, as large felids occasionally leave a considerable amount of scavangeable flesh and within bone tissue following carcass processing (Pobiner, 2007). However, if the two ungulate ribs detailed in Roberts et al. (2018; Chapter Three) and the elephant rib described in the present study represent genuine cut-marked bones, it would suggest that hominins had, at least on occasion, primary access to medium- as well as large-sized animal carcasses as these elements are quickly destroyed by carnivores during evisceration (Blumenschine, 1986; Domínguez-Rodrigo, 1999). If hominins were actively hunting in the western Nefud Desert, the low anthropogenic signal in the Unit 5 fossil assemblage may be explained by off-site carcass processing – as proposed by the "nearkill location" and "refuge" models (Blumenschine, 1991; Blumenschine et al., 1994; O'Connell, 1997; O'Connell et al., 2002). These models posit that early hominins transported carcasses, or some portion of them, away from kill sites (often surrounding rivers and lakes) to nearby protected areas to avoid/delay competition with other carnivores; a method employed by modern huntergatherer groups (e.g. Hadza [Bunn et al., 1988; O'Connell et al., 1992]). Given the open grassland lakeshore setting, and the presence of large and potentially dangerous carnivores, hominins in the western Nefud may have benefited from such a subsistence strategy.

In contrast to the Unit 5 assemblage, the surface fossil deposits (TSR, TIL, TLS) assessed here are poorly preserved and heavily fragmented, and, as such, far less can be reliably said about their accumulation. Wind abrasion has affected much of these assemblages, while other attritional processes such as salt and insolation weathering may have further degraded the fossils (see also *Chapter Six*). Carnivores played at least some role in the

accumulation of these assemblages, and it seems likely that their role was greater than the current bone surface modification data suggests. Lastly, we note that hominins, too, may have played a role in the accumulation of the TSR assemblage, as suggested by notches and grooves redolent of cut and hammerstone percussion marks. The recovery of lithic artefacts alongside fossils evokes hominins as potential accumulators of fossils around the lake at Ti's al Ghadah. Significantly, the lithic artefact assemblages associated with various phases of lake formation indicate repeated use of the Ti's al Ghadah basin by hominins during pluvial phases of the Pleistocene and, as previously stated by Scerri et al (2015), may represent the earliest Middle Palaeolithic assemblage in Arabia.

CONCLUSIONS

The Unit 5 assemblage of Ti's Al Ghadah, and accompanying sedimentological evidence, suggest that the deposit represents a predation hotspot where large felids and probably hominins ambushed mostly mediumsized ungulates in a lakeside environment, while more durophagous carnivores such as hyenas and canids occasionally scavenged from large felid kills. Less can be said about the other assemblages present in the basin, but the evidence preserved suggest that they too were accumulated by, at the very least, non-hominin carnivores in a lakeside environment. This study provides the first detail insights into the interplay between hominins, carnivores, and herbivores in Arabia, and suggests that watering holes have been a focus on the Arabian landscape for resources since the middle Pleistocene.

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Figure S1 (*above*). Summary diagram of Ti's al Ghadah Iron Lake (TIL) diatom assemblage. All taxa with relative abundances of ≥ 2 % are shown. Diatoms are ordered according to their weighted averaging distribution. The planktonic:benthic ratio is shown with the habitat summary, log concentration, F-index (ranging from 0 [most dissolved] to 1 [most pristine]). Due to the low concentration of diatoms in this lake, only the lower sample contains the representative number of valves. The log concentration and F-value shows the diatoms present for all samples analysed including samples where the taxa are too low to be representative for inferring conditions at the site.

Figure S2 (below). Summary diagram of Ti's al Ghadah Unit 6 diatom assemblage. All taxa with relative abundances of ≥ 2 % are shown. Diatoms are ordered according to their weighted averaging distribution. The planktonic:benthic ratio is shown with the habitat summary, log concentration, F-index (ranging from 0 [most dissolved] to 1 [most pristine]). Due to the low concentration of diatoms in this lake the upper sample does not contain the representative number of valves. The log concentration and F-value shows the diatom valves and chrysophyte scales present for all samples analysed including samples where the taxa are too low to be representative for inferring conditions at the site.





Appendix B. Taxonomic and taphonomic analysis results

Figure S3: Upper 2nd molar length (A) and width (B) and upper 3rd molar length (C) and width (D) measurements of fossil teeth from Unit 5 and comparative morphometric data from various species of Alcelaphinae [data from Louys et al. (2015) and comparative material housed at the Smithsonian NMHH].



Figure S4. Lower 2^{nd} molar length (A) and width (B) and lower 3^{rd} molar length (C) and width (D) measurements of fossil teeth from TSR and comparative morphometric data from Unit 5 and various species of extant *Oryx* (data from comparative material housed at the Smithsonian NMHH).



Figure S5. Distribution of frequencies (%NISP) for each specimen size range for the TLS and TSR assemblages.

Element	Tre	nch 1	Trer	nch 2	Trer	nch 4	Trer	nch 5	Tren	ich 6
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Cranium	10	4	_	_	_	_	4	4	7	3
Horn core	3	2	_	_	_	_	1	1	3	2
Mandible (one side)	16	9	_	_	_	_	2	2	8	3
Teeth	5	5	1	1	1	1	7	7	11	11
Atlas	2	2	_	_	_	_	2	2	_	_
Axis	3	3	_	_	_	_	1	1	1	1
Cervical vertebrae	8	8	_	_	_	_	_	_	_	_
Thoracic vertebrae	9	6	2	2	_	_	1	1	_	-
Lumbar vertebrae	1	1	_	_	1	1	_	_	1	1
Caudal vertebrae	_	_	_	_	_	_	_	_	_	_
Indeterminate vertebrae	_	_	—	_	—	_	—	_	_	—
Rib	16	2	1	1	_	_	3	1	2	1
Sacrum	2	_	_	_	_	_	_	_	1	1
Sternum	—	_	—	—	—	—	—	—	—	—
Scapula	10	4	_	-	1	1	1	1	1	1
Pelvis	2	1	_	-	-	-	2	1	2	1
Humerus	1	1	_	_	_	_	2	2	2	2
Radius	2	2	—	—	—	—	1	1	2	2
Ulna	3	3	_	-	-	-	3	3	1	1
Metacarpal	5	5	_	-	-	-	5	3	-	-
Femur	2	1	_	_	_	_	_	_	1	1
Tibia	4	4	_	_	_	_	7	6	1	1
Fibula	_	_	_	_	_	_	_	_	_	—
Patella	1	1	_	_	-	-	_	-	_	-
Astragalus	1	1	1	1	_	_	_	_	2	2
Calcaneus	1	1	_	-	-	-	-	-	1	1
Carpal / tarsal	3	3	1	1	1	1	1	1	2	2

Table S1. Unit 5 medium-sized ungulate skeletal part representation according to NISP and MNE.

Element	Tre	nch 1	Trer	ich 2	Tren	nch 4	Trer	nch 5	Trer	nch 6
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Metatarsal	_	_	_	_	_	_	7	6	2	2
Indeterminate metapodial	2	_	1	1	1	1	_	_	_	_
Indeterminate midshaft	1	_	_	_	_	_	_	_	_	_
Phalanges	_		_	_	_	_	_	_	_	_
- Proximal	4	4	2	2	—	_	—	_	1	1
- Intermediate	3	3	—	—	—	_	1	1	_	_
- Distal	—	_	—	—	—	_	—	_	_	_
Sesamoid	—	_	—	—	—	_	—	_	_	_
Indeterminate MSHF	1		_		_		_		_	
Total	121	76	9	9	5	5	51	44	52	40

Table S2. Unit 5 small- and medium-sized bovid limb bone portion abundance (MNE) and corresponding goat and wildebeest bone mineral density (ρ) values according to density scan site. Density of small- and medium-sized bovid bones based on goat (Lam et al., 1998) and wildebeest (Lam et al., 1999) bone mineral density, respectively.

		Small-size	d bovid	Medium-sized bovid		
		Density (ρ)	MNE	Density (p)	MNE	
Hume	erus		2	-	4	
-	HU1	0.30	0	0.32	0	
-	HU2	0.34	0	0.49	0	
-	HU3	1.15	2	1.10	4	
-	HU4	0.98	1	1.03	4	
-	HU5	0.56	0	0.51	4	
Radiv	IS		1		5	
-	RA1	0.66	1	0.51	5	
-	RA2	1.03	0	1.02	5	
-	RA3	1.17	0	1.07	5	
-	RA4	0.86	0	0.96	3	
-	RA5	0.52	0	0.47	4	
Metac	carpal		1		9	
-	MC1	0.75	1	0.72	9	
-	MC2	1.04	1	1.12	9	
-	MC3	1.06	1	1.15	9	
-	MC4	0.83	1	0.83	5	
-	MC6	0.61	1	0.62	2	
Femu	r		0		0	
-	FE2	0.61	0	0.51	0	
-	FE3	0.66	0	0.92	0	
-	FE4	0.66	0	0.92	0	
-	FE5	0.56	0	0.66	0	
-	FE6	0.50	0	0.38	0	
Tibia			1		11	
-	TI1	0.41	0	0.49	4	
-	TI2	0.76	0	0.91	3	
-	TI3	1.24	0	1.12	11	
-	TI4	1.04	0	1.09	10	
-	TI5	0.60	0	0.59	11	
Metat	arsal		0		8	
-	MR1	0.85	0	1.11	8	
-	MR2	1.14	0	1.11	8	
-	MR3	1.13	0	1.14	8	
-	MR4	0.90	0	0.54	3	
-	MR6	0.63	0	0.65	3	

Table S3. Unit 5 small- and medium-sized bovid skeletal part representation and corresponding standard food utility index (SFUI) values for low- and high-survival survival elements [data from Metcalfe and Jones (1988)].

Element	SFUI	Small-sized	Medium-sized									
(low- and high-		bovid	bovid									
survival)		MNE	MNE									
Mandible	31.1	1	14									
Atlas	10.2	0	4									
Axis	10.2	0	4									
Cerv. vert.	37.1	0	5									
Thor. vert.	47.3	0	8									
Lumb. vert.	33.2	0	3									
Pelvis	49.3	0	3									
Rib	51.6	0	2									
Scapula	66.6	2	4									
Prox. humerus	44.7	0	0									
Dist. humerus	36.8	2	4									
Prox. radius	25.8	1	6									
Dist. radius	20.2	0	4									
Prox. metacarpal	9.0	1	9									
Dist. metacarpal	7.1	1	2									
Prox. femur	100.0	0	0									
Dist. femur	100.0	0	0									
Prox. tibia	62.8	0	4									
Dist. tibia	44.1	0	11									
Astragalus	27.7	1	24									
Calcaneus	27.7	0	23									
Prox. metatarsal	19.5	0	58									
Dist. metatarsal	15.4	0	53									
Prox. phalanx	8.6	1	27									
Int. phalanx	8.6	0	4									
Dist. phalanx	8.6	1	0									
Element	SFUI	Small animal	Medium animal									
(high-survival only)		MNE	MNE									
Crania	9.1	1	11									
Mandible	11.5	1	14									
Humerus	36.8	2	4									
Radius	25.8	1	6									
Metacarpal	5.2	1	9									
Femur	100.0	0	0									
Tibia	62.8	0	11									
Metatarsal	37.0	0	8									
Element	Small-sized animal NISP		Medium-sized animal NISP		Large-sized animal NISP			Indeterminate-sized animal NISP				
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	ТМ	CM?	PM?	TM	CM?	PM?	TM	CM?	PM?	TM	CM?	PM?
Cranium	1			3						1		
Mandible (one				2								
side)												
Teeth				1								
Clavical	1											
Atlas				2								
Cerv. vert.				1								
Thor. vert				4								
Lumb. vert				1								
Rib	1			25	2					5		
Scapula	1			6								
Pelvis	1			3						1		
Humerus	5			2								
Radius	2			3								
Ulna				3						1		
Metacarpal	1			4		1						
Femur	1			2								
Tibia				9		1						
Calcaneus				2								
Metatarsal				4								
Indet. midshaft				6		1						
Prox. phalanx												
Indet. frag.										4		
Total	14	0	0	86	2	3	1	0	0	12	0	0

Table S4. Unit 5 tooth-marked (TM), probable cut-marked (CM?), and percussion-marked (PM?) bones for small-, medium-, and large-sized animals.

Element		Trench 1 NISP		I	Trench 2 NISP			Trench 4 NISP			Trench 5 NISP	•		Trench 6 NISP	Í
	TM	CM?	PM?	TM	CM?	PM?	TM	CM?	PM?	TM	CM?	PM?	ТМ	CM?	PM?
Cranium	4												1		
Mandible	2												1		
(one side)															
Teeth															
Clavical	1														
Atlas	1									1					
Cerv. vert.	1														
Thor. vert	3			2											
Lumb. vert													1		
Rib	18	1		1			1			1	1		5		
Scapula	4									2			1		
Pelvis	1									2			2		
Humerus	4						1						1		
Radius	2									2			1		
Ulna	1									2			1		
Metacarpal			1							4			1		
Femur	2									1					
Tibia			1							8			1		
Calcaneus	1												1		
Metatarsal										3			1		
Indet.	3		1												
midshaft															
Prox.	1												1		
phalanx															
Indet. frag.							1						3		
Total	49	1	3	3	0	0	3	0	0	27	1	0	24	0	0

Table S5. Unit 5 tooth-marked (TM), probable cut-marked (CM?), and percussion-marked (PM?) bones broken down by trench.

CHAPTER FIVE

Human footprints provide snapshot of penultimate interglacial ecology in the Arabian interior

Mathew Stewart

The project was conceived and led by MS. MS conducted the fossil, ichnofossil, and imaging analysis, Richard Clark-Wilson conducted the sedimentary and dating analysis, Patrick Roberts conducted the isotope analysis, and David Ryves conducted the diatom analysis. MS prepared the manuscript.

ABSTRACT

When exploring questions surrounding hominin evolution, behaviour, and demography, it is often important to consider the immediate ecological settings in which these hominins lived. However, reconstructing past ecologies based on associated fauna, isotopic data, phytolith analysis, and the like, typically provides resolution at scales of hundreds or thousands of years, especially as we attempt to look further and further back in time. The unique setting and taphonomic factors affecting the long-term preservation of tracks (or footprints) means that groups of tracks can be confidently assumed to have been generated within a very short window, usually within a few hours or days. As a result of this, tracks and trackways can offer rare glimpses into the interplay between hominins, animals, and their immediate surroundings not afforded from the archaeological and fossil record alone. Here I describe hominin and non-hominin mammal tracks and trackways (as well as fossils) from the Alathar palaeolake deposit in the western Nefud Desert, northern Saudi Arabia. Tracks were dated to c. 121–112 ka. Analysis of the palaeolake sediment indicates that the lake was fresh throughout its existence. Freshwater lakes would have provided a vital resource and habitable landscape for both hominins and mammals within the Arabian interior. Abundant large herbivore tracks document intensive use of the lake over a very short period, probably reflecting a dry period. The hominin tracks indicate the presence of a numerous adult individuals engaged in non-directional activities, perhaps visiting the lake to drink and/or forage for plant foods. Importantly, this suggests that hominin and large mammals were occupying the same space and utilising the same freshwater resources across short time scales. Considering the apparent absence of Homo neanderthalensis from the broader region until after c. 80 ka, it is argued that *H. sapiens* is responsible for the Alathar tracks.

INTRODUCTION

Southwest Asia (extending from the Arabian Peninsula to the south, Anatolia to the west, southern Caucasus Mountains to the north, and Iran to the west) represents the key biogeographical gateway between Africa and Eurasia (O'Regan, et al., 2011) and is therefore important for understanding faunal and hominin dispersal and evolution across continents. During the late Pleistocene, the region was home to at least two hominin species – Homo sapiens and H. neanderthalensis – and genetic data suggest that these groups interbred in the region (Green et al., 2010; Sankararaman et al., 2012). Indeed, a highly dynamic picture of *H. sapiens–H. neanderthalensis* interactions and movements within southwest Asia is now emerging (see Bae et al., 2017 for recent review). Archaeological data indicates that Homo was widespread across the Arabian Peninsula during the late Pleistocene (Armitage et al., 2011; Delagnes et al., 2012; Petraglia et al., 2012; Crassard et al., 2013; Groucutt et al., 2015; Scerri et al., 2015) and recent fossil evidence demonstrates the arrival of H. sapiens in the Arabian interior by c. 90 ka (Groucutt et al., 2018), marking the oldest unambiguous record of our species outside Africa and the Levant.

Occupation of the Arabian interior during the late Pleistocene appears to have been restricted to interglacial and interstadial periods (Groucutt and Petraglia, 2012; Breeze et al., 2017) which brought enhanced humidity and precipitation over the peninsula (Fleitmann et al., 2011; Jennings et al., 2015). Yet, palaeoenvironmental and palaeoecological reconstructions are typically based on proxies that provide resolution at scales of hundreds or thousands of years (e.g. Fleitmann et al., 2011; Jennings et al., 2015), making inferences on the immediate ecology of late Pleistocene *Homo* populations in Arabia difficult. Even in instances where hominin artefacts and fossil fauna have been found alongside one another, their exact relationships have remained ambiguous (e.g. Scerri et al., 2015). For surface deposits, which represent a large percentage of the Arabian palaeontological and archaeological record, the situation is worsened by rapid sediment deflation, resulting in potentially deeply time-averaged fossil and stone tool assemblages (see *Chapters Four & Six*).

Tracks and trackways (that is, prints and sets of prints generated by an individual) provide unique opportunities to investigate locomotion, behaviour, and hominin-animal-environment interactions across very short time intervals (e.g. Renders, 1984; Webb et al., 2006; Hatala et al., 2016, 2017a, 2017b; Roach et al., 2016, 2018; Altamura et al., 2018). The taphonomic factors affecting long-term preservation of tracks means that groups of stratigraphically associated tracks, and particularly those in similar states of preservation, can be assumed to have been generated within a very short window, usually within a few hours or days (Cohen et al., 1991; Roach et al., 2016). An experimental study of modern human footprints in mud flats found that fine details were lost within two days and prints were rendered unrecognisable within four (Roach et al., 2016). Similar observations have also been made for other non-hominin mammal tracks (Cohen et al., 1991). Physical variables mediating track formation and preservation include substrate properties (e.g. grain size, water content), erosion, desiccation, precipitation, and compaction, while biological variables include body mass, behaviour, trampling, and bioturbation (see Cohen et al., 1994 and Bennett and Morse, 2014 for detail discussion on the physical and biological processes affecting track formation and preservation). Tracks in circum-lacustrine settings, which are common in the ichnofossil record due to the conduciveness of fine-grained muddy sediments for track formation, are further subjected to seasonal lake level fluctuations, daily wave and seiche action, repeated desiccation events, and microbial mat development (i.e. sheets of bacteria and/or archaea that develop within prints) (Cohen et al., 1991; Marty et al., 2009). Following exhumation, tracks undergo rapid degradation resulting in their swift removal from the ichnofossil record (Ashton et al., 2014; Wiseman and Groote, 2018; Zimmer et al., 2018). Considering the suite of independent and interactive processes affecting long-term preservation of tracks, it should come as no surprise that they are rarely preserved in the geological record (Bennett and Morse, 2014).

Hominin track-bearing sites are especially rare and those dating to the Mio-Plio-Pleistocene number around thirty (Appendix C). Nonetheless, they have provided remarkable insights into hominin locomotion and behaviour that cannot be gleaned from the archaeological and palaeontological record alone. The Laetoli Bed footprints at Laetoli, Tanzania, provided the earliest definitive evidence for bipedal locomotion among Pliocene hominins (Leakey and Hay, 1979; Day and Wickens, 1980; Raichlen et al., 2010; Crompton et al., 2011; Hatala et al., 2017a). The Ileret footprints, Kenya, demonstrated that by 1.5 million-years-ago *H. erectus* had developed a foot form and gait comparable to H. sapiens (Bennett et al., 2009; Hatala et al., 2016). Hominin prints were found to be disproportionately abundant at Ileret, suggesting intensive use of lake margin habitats (Roach et al., 2016, 2018). Moreover, these tracks have been interpreted as multi-male groups moving in concert through the landscape, providing credible evidence for labour division and male-male cooperative behaviour in early Pleistocene hominins (Roach et al., 2016; Hatala et al., 2017). Footprints dated to c. 700 ka at the site of Gombore II-2, Ethiopia, document the repeated use of the lake margin by adults and children over a very short time, probably within a single season (Altamura et al., 2018). Those tracks, coupled with onsite evidence for carcass butchery, suggest mixed-aged family groups were cooperatively foraging around the

299

lake margin (Altamura et al., 2018). Webb et al. (2006) made similar observations from the adult and juvenile late Pleistocene *H. sapiens* footprints at Willandra lakes, Australia. Tracks and trackways have therefore shown great potential for providing unique insights into various aspects of early hominin life, particularly for understanding their social structure and behaviour.

Here I report *H. sapiens* and non-hominin mammal tracks, as well as fossils, from the Alathar lacustrine deposit in the western Nefud Desert, Saudi Arabia (Fig. 1), dated to the penultimate interglacial. Significantly, these tracks represent the earliest dated evidence of our species in the Arabian Peninsula. In addition to studying the footprints themselves, this study aims to develop a depositional model of the lake sediments through the analysis of the sedimentary sequence, thin-sections, and diatom assemblages, as well as provide insights into the environment (humidity, vegetation) through isotope analysis of fossil herbivore teeth.

METHODS

Site stratigraphy and sedimentology

Macroscale sedimentology

Two sedimentary sections were logged at the site and a composite section formed (Fig. 2). The two sections are located ~10 meters apart, and the relationship between them is clearly visible in the field. The first section (Section 1; 142 cm in height; Units 2–4) is located on the western margin of the relict palaeolake deposit and facing the lee side of the dune. Here the palaeolake sequence is the thickest, suggesting the lake depocenter lie toward the southwest but has since been eroded. Stratigraphically above Section 1 a second section (Section 2; 39 cm in height; Units 5–7) was located near the centre of the modern-day surface of the palaeolake deposit. Each section was logged and described to determine the sedimentary structure (e.g. bedding, units) and texture (e.g. sorting, grain size, colour). Samples for laboratory analysis were collected by extracting coherent blocks from the sedimentary section.

Micromorphology

Thin-sections for petrographic analysis were prepared from fresh sediment blocks, subsampled from coherent blocks collected in the field, following standard thin-section preparation techniques developed in the Centre for Micromorphology at Royal Holloway University of London (Palmer, 2008). Thin sections were analysed using an Olympus BX-50 microscope with magnifications from 20x to 200x and photomicrographs were captured with a Pixera Penguin 600es camera. 120 thousand-year-old footprints



Figure 1. (A) Map displaying the study area (red star) within the western Nefud Desert. (B) Map of the Alathar site displaying the location of hominin and nonhominin tracks.

Optically stimulated luminescence (OSL) dating

Sample collection and preparation

Three samples were collected for luminescence dating. One sample (PD60) was taken from the underlying aeolian dune sands (Unit 1), another sample (PD61) from Unit 2 within the main palaeolake sequence, and a final sample (PD62) from Unit 5, which stratigraphically overlies the footprints and *in situ* fossils (Fig. 2). PD60 was taken by hammering an opaque tube into a cleaned section face, whereas PD61 and PD62 were extracted as consolidated blocks. Samples were prepared under subdued red light in the Royal Holloway Luminescence Laboratory. First the sunlight exposed external portions of the sample were removed and retained for dose rate

evaluation, leaving a sub-sample suitable for dating. The sample for dating was immersed in 10% HCl to remove carbonate, but since no organic matter was present, samples were not treated with H₂O₂. The remaining mineral fraction was disaggregated in dilute sodium hexametaphosphate solution and wet-sieved to 180–210 μ m. Quartz was extracted from the retained fraction using density separations at 2.75 and 2.62 g/cm3 and a subsequent HF acid etch (23M HF for 60 min followed by a 24-hour immersion in 10M HCl). Etched samples were re-sieved at > 150 μ m, to remove partially dissolved grains, and stored in opaque containers prior to measurement. Before measurement, the purified quartz was mounted as a monolayer on a 10 mm diameter stainless steel disc using Silkospray oil applied via a 5 mm mask.

<u>Equipment</u>

All luminescence measurements presented here were carried out using a Risø TL/OSL-DA-15 automated dating system (Bøtter-Jensen et al., 2003). Optical stimulation of single-aliquots used blue light emitting diodes emitting at 470 nm with a stimulation power of 69.4 mW/cm². All infra-red (IR) stimulation was carried out using an IR (870 nm) laser diode array yielding a power density of 206 mW/cm². OSL passed through 7.5 mm of Hoya U-340 filter and was detected using an Electron Tubes Ltd 9235QB15 photomultiplier tube. Irradiation was carried out using a 40 mCi ⁹⁰Sr/⁹⁰Y beta source giving ~6 Gy/min. This source is calibrated relative to the National Physical Laboratory, Teddington ⁶⁰Co Y-source (Hotspot 800, Armitage and Bailey, 2005).

Single-aliquot measurement and analysis

Equivalent doses (D_e) were estimated by measuring 48 aliquots of each sample using the single-aliquot regenerative-dose (SAR) method (Murray and 303 Wintle, 2000). To ensure that the measurement conditions were optimal, dose recovery tests (Roberts et al. 1999) were performed on samples PD61 and PD62 using a known dose of ~108 Gy. A preheating regime of 200°C held for 10 seconds prior to the measurement of the natural (L_n) /regenerated (L_x) signal, and 160°C held for 5 seconds prior to measurement of the test dose (T_x) signal gave dose recovery ratios of 1.02 ± 0.02 for PD61 and 1.01 ± 0.04 for PD62. This preheating regime was therefore suitable for subsequent D_e measurements. Optical stimulation was carried out at 125°C for 60 seconds using blue LEDs. The OSL signal was calculated from the signal from the first 0.32 seconds of stimulation, with a background signal estimated from the last 4 seconds of the decay curve subtracted. Except where noted below, dose response curves (DRC) were fitted with a saturating-exponential-pluslinear function, and the standard error associated with each individual D_e determination was estimated by Monte Carlo simulation (1000 simulations). D_e determination, curve fitting and Monte Carlo simulation were performed using Luminescence Analyst software version 4.31.9 (Duller, 2007).

Data from individual aliquots were rejected where the aliquot yielded either an IR depletion ratio >2 σ below unity (Duller, 2003) or a recycling ratio >2 σ different from unity (Murray and Wintle, 2000). These tests reject aliquots with significant feldspar contamination, or which have poor luminescence properties respectively. In addition, aliquots yielding natural luminescence intensities greater than the saturation level of the growth curve (i.e. "oversaturated" aliquots) were rejected. Although a considerable body of literature concerning "oversaturated" aliquots exists, there is little consensus on the most appropriate method for dealing with this phenomenon. In the present instance, sensitivity tests were performed with three variations of acceptance criterion relating to oversaturation (Table S1): (1) accept all aliquots for which Analyst generates a finite D_e; (2) reject those aliquots yielding natural luminescence intensities (L_n/T_n) which exceed the saturation point of a single saturating exponential fit through the data (using Analyst version 4.31.9) or exceed 15% of the L_x/T_x of the highest-dose regeneration point when fitted with a saturating-exponential-plus-linear function; (3) reject all aliquots yielding natural luminescence intensities (L_n/T_n) exceeding twice the curve fitting parameter D_0 when the DRC is fitted using a single saturating exponential function (Wintle and Murray, 2006). Approach 1 includes very high D_e values and probably overestimated D_e due to the incorporation of saturated aliquots. This approach may be regarded as generating a maximum age. Approach 3 excludes aliquots yielding high D_es, some/many of which may provide accurate estimates of the absorbed dose. This approach may be regarded as generating a minimum age (see Wintle and Adamiec, 2017, p. 24 for discussion). Approach 2 is effectively a less stringent version of Approach 3, and in the present study always yields D_e values lying between the other two options. Consequently, it is suggested that Approach 2 best represents the true absorbed dose. All burial doses were estimated using this approach.

Details of accepted and rejected aliquots are presented in Table S2. Briefly, rejection criteria were applied in order, with only one rejection criterion being recorded per aliquot. Of the 144 aliquots measured, 2 failed the recycling ratio test, 68 failed the IR-depletion ratio test and 10 were oversaturated, leaving 63 accepted aliquots. Several previous studies of quartz from the Nefud Desert have reported similarly high IR-depletion ratio test failure rates (e.g. Petraglia et al., 2012; Groucutt et al., 2018).

To determine the age of a sample, a single-burial dose (D_b) must be calculated from the accepted single-aliquots. As the samples represent wellbleached aeolian dune sands, or sands derived from such sands, D_b was calculated for all samples using the central age model (CAM) in the R luminescence package (Galbraith et al., 1999; Burrow, 2017). Overdispersion values ranged from 27±5 to 39±5 %. These are relatively high for singlealiquot samples from aeolian dune sands (PD60) and sands within the lake sediments that derive from the surrounding dunes (PD61 and PD62). The main cause of overdispersion in these samples is unclear. Partial bleaching is unlikely to have occurred in the case of the aeolian sand sample (PD60), and the sand in samples PD61 and PD62 are likely to have been introduced to their depositional environment via aeolain/fluvial mobilisation of wellbleached surficial sands. Post-depositional mixing ("bioturbation") of samples PD61 and PD62 is unlikely given that both were consolidated via desiccation shortly after deposition, precluding the introduction of much younger/older grains. Beta microdosimetry alone has recently been shown to be capable of causing single-grain overdispersion exceeding 25% (Armitage et al., in press), and is regarded as the primary cause of the high values measured in the present study. This inference is supported by the low environmental dose rates for Alathar palaeolake samples (0.4–1.1 Gy/ka) while there is a low concentration of K-feldspar identified by XRD analysis. Modelling by Mayya et al. (2006) has demonstrated that these factors (i.e. low total does rate combined with the presence of K-feldspars) may yield high overdispersion values even for well-bleached, unmixed sediments, since the sparse Kfeldspars act as local "hotspots" of beta dose. This scenario is regarded as the most plausible explanation of the high overdispersion observed in our datasets, in which case the CAM is the most appropriate age model to use for the Alathar palaeolake samples. See Table 1 for summary dating results and ages.

Environmental dose rate calculations

The environmental dose rate for HF etched quartz grains consists of external beta, gamma and cosmic ray components (Table S3). Beta dose rates were measured using a Risø GM-25-5 low-level beta counting system (Bøtter-Jensen and Mejdahl, 1988), using MgO and Volkagem loess (De Corte et al., 2007) standards. Gamma dose rates were measured in the field using an EG&G Ortec digi Dart-LF gamma-spectrometer using the "threshold" method. Dose rates were corrected for beta attenuation (Mejdahl, 1979), the etch depth (Bell, 1979), grain size and a water content of $5\pm2.5\%$. The 2σ uncertainty on water content encompasses completely dry conditions and saturation for 25% of the burial period (10%), representing the full range of reasonable mean water content scenarios of a freely draining aeolian sand. Cosmic ray dose rates were calculated using site location (27N, 39°E, ~955 m elevation) and present-day sediment burial depths (Prescott and Hutton, 1988), assuming a sediment overburden density of 1.80 g/cm³. The total environmental dose rate and final age estimates were calculated using Dose Rate and Age Calculator (Durcan et al., 2015).

Diatom analysis

Diatom analysis was carried out on three samples spanning the sequence, at 40 cm (Unit 2), 140 cm (Unit 4b), and 175 cm (Unit 7) above the base level. Standard methods were employed on untreated sediment subsamples to make strewn slides (Renberg 1990), heating samples in concentrated H_2O_2 , washing 4 times in distilled water before settling onto coverslips before permanent slides were made, mounted in a high contrast medium (Naphrax). Diatoms were counted under oil immersion with phase contrast illumination at x1000. Quantitative reconstructions were carried out

using the programme C2 (v1.7.7; Juggins, 2016 available at *https://www.staff.ncl.ac.uk/stephen.juggins/softwareC2Home.htm*).

Analog matching of fossil samples was performed within the combined African salinity dataset (n=370) from the European Diatom Database (EDDI; <u>http://craticula.ncl.ac.uk/Eddi/jsp/;</u> Juggins, 2001), which includes modern samples from northern and eastern Africa (Gasse et al., 1995). As the closest analogues in all cases were from East African sites (n=179), the East African subset of the database was used for our conductivity reconstructions. Inferred conductivity (μ S cm⁻¹) was derived from fossil assemblages (% data) using a weighted-average transfer function with inverse de-shrinking. The conductivity model performs well when internally validated by leave-one-out jack-knifing ($r^2_{jack} = 0.784$, RMSEP = 0.41 log units) and provides sample-specific errors on diatom-inferred conductivity.

There is good coverage between fossil and modern training sets. Goodness-of-fit was assessed by considering the proportion of fossil data used in each sample for reconstructions, and the minimum dissimilarity coefficient (MinDC) between each fossil sample and the training set. Other studies have suggested that good analogues exist in a training set where MinDC is 100– 150 or less (Jones and Juggins, 1995; Juggins, 2001).

Fossil and ichnofossil analysis

Fossils were systematically collected during pedestrian line surveys across the site and their position recorded using a Differential Global Positioning System (DGPS). Pedestrian surveys were conducted by three to five people walking together in a straight line and separated by no more than two meters. The entire exposure of the palaeolake was examined and all fossils regardless of size and preservation were collected. A small number of fossils (n=4) were found eroding out of the palaeolake sediments and were carefully retrieved using trowels and brushes (e.g. Fig. 6J). Each fossil specimen was identified to the lowest taxonomic level possible and facilitated by osteological collections housed at the University of New South Wales, Australia (UNSW). Taphonomic analysis was carried out following the methods described in *Chapters Three* and *Four* (Stewart et al., 2019).

Footprints were systematically documented during pedestrian surveys across the site and their position recorded using a Leica Total Station (Fig. 1). Each print was photographed with a scale, compass, and arrow denoting orientation of movement when discernible (e.g. Fig. 6), and length and width measurements were recorded. Where necessary, windblown infill was carefully removed using a soft brush. Directionality was assessed using Rayleigh's Z test for uniformity for circular data and a Watsons U² test for von Mises normal distribution.

Three hominin prints (HPR001, HPR002, HPR003) were extensively photographed in order to generate high-resolution, scaled 3D models (AgiSoft Photoscan Professional, AgiSoft, LLC, St. Petersburg, Russia). Photography was conducted during both the morning and afternoon to capture the prints under varying lighting conditions and allow for *post hoc* selection of the most suitable set. Additional TS points (~15 points for each) were taken to map the print outline, as well as high and low points in and around the prints which acted as ground control points (GCPs) during model generation (note that the accuracy of the TS point data provides absolute measures, and, therefore, the error associated with these is negligible and is not reported). Print morphometric data was collected in the field following Bennett et al. (2009) (Fig. 7A). It should be noted, however, that some of the prints are poorly preserved (e.g. HPR003, HPR005) and these measurements should be considered estimates. Footprint index (FPI) was calculated by dividing footprint length (Heel-Hallux) by ball breadth (B1-B2). Hominin stature, body mass, and speed estimates were calculated following Dingwall et al. (2013) and based on regression equations derived from footprint morphometric data of modern, habitually unshed Daasanach people (Lake Turkana region, Kenya). Stature was determined from footprint length (FPL), body mass from footprint area (FP area = FPL*BW), and speed from stride length (SL; distance from the heel of one step to the heel of the next step made by the same foot) divided by average footprint length (SL/avgFPL). Comparative stature and mass data for late Pleistocene *H. sapiens* (n=89) and *H. neanderthalensis* (n=50) was sourced from the literature and based on allometric relationships between limb bone size and body height (data from Feldesman et al., 1990; Carretero et al., 2012 Will et al., 2017; Ruff et al., 2018). Values were averaged in instances where multiple estimates existed for a single individual (e.g. the Skhul IV hominin).

Sex determination estimates were calculated following the stepwise multivariate discriminant function analysis detailed in Abledu et al. (2015; eqn 1) using two parameters for left prints (i.e. Heel–D5 and H1–H2) and three parameters for right prints (i.e. Heel–Hallux, B1–B2 and H1–H2). An individual print was classified as representing a male if the discriminant function (*D*) was greater than the sectioning point (*S*), and female if *D* was smaller than *S* (left footprint S = -0.149, right footprint S = -0.084).

$$D = b_o + \sum_i b_i X_i \qquad [1]$$

Where b_0 and b_i represent coefficients of the discriminant function analysis and X_i represents footprint measurement.

Stable carbon and oxygen isotope analysis

Stable carbon and oxygen isotope analysis was carried out following the protocol outlined in *Chapter Three* (Roberts et al., 2018). Eight samples (seven bovid teeth and one elephant tooth) were selected for δ^{13} C and δ^{18} O isotope analysis of tooth enamel from the available fossil material recovered from atop modern-day palaeolake deposit.

RESULTS

Site stratigraphy and sedimentology

The Alathar deposit is an inverted relief lake sediment sequence found within an interdunal depression in the Nefud Desert sand sea. The sedimentary sequence comprises a ~1.8 m thick deposits of sandy-silt diatomite (Units 2–7) underlain by windblown sands (Unit 1) (Fig. 2). The topography of the deposit is well preserved with a subtle concave shape dipping toward the centre of the remaining palaeolake deposit.

Macroscale sedimentology

Unit 1 is formed from well-sorted wind-blown dune sands. The first palaeolake section consists of three discrete units (Units 2–4). Unit 2 is ~65 cm thick and consists of loosely consolidated sandy-silt diatomite with some evidence for horizontal bedding. There is also evidence of orange coloured, thin, elongate mottling. Unit 3 is ~35 cm thick and is characterised by horizontally-bedded sandy-silt diatomite that interdigitates with sand layers. Obvious orange mottling continues, as does centimetre-scale root casts that run between the horizontal diatomite bedding planes. Unit 4 is ~42 cm thick and is split into two sub-units. Unit 4a (100–125 cm) is formed of consolidated

and horizontally bedded sandy-silt diatomite that interdigitates with laterally continuous sand layers. There is no evidence of mottling or root casts, while the sediment is almost pure white. Unit 4b (125–142 cm) is a structureless, pure white sandy-silt diatomite that is consolidated, has no horizontal bedding features, and contains desiccation cracks. It is in this upper surface of this unit that footprints and *in situ* fossils were found.

The second section (142-179 cm; Units 5-7), which lies ~10 m from the first section and stratigraphically above it and therefore the prints, is divided into three units. Unit 5 is ~21 cm thick and consists of a sandy-silt diatomite that interdigitates with bedded sands. Unit 6 is ~14 cm thick and is composed of sands with laterally discontinuous but consolidated sandy-silt diatomite beds with reworked rip-up diatomite clasts. The uppermost Unit is ~4cm thick and is composed of homogenous sandy-silt diatomite.

Further laboratory analysis was carried out to determine calcium carbonate content and bulk mineralogy. To measure calcium carbonate content, sub-samples of between 0.2 - 0.5 g were removed, powdered, and analysed using Bascoomb calcimetry (Gale and Hoare, 1991). This demonstrated there was no carbonate within the sedimentary sequence. Bulk mineralogy was analysed using whole rock X-ray diffraction (XRD). Powdered samples were mounted as a thin monolayer on glass slides and analysed on a Philips PW1830/3020 spectrometer with copper K α X-rays. Mineral peaks were identified manually from the ICDD Powder Diffraction File database. XRD analysis shows that quartz is the predominant mineral with a percentage of either 90-100%, with k-feldspars the only other mineral present in the analysis. This contrasts with other MIS 5 palaeolake deposits in the western Nefud Desert that are carbonate rich (e.g. Al Wusta; Groucutt et al., 2018)

Micromorphology

Fourteen thin-sections were taken across both sections (Fig. 3) and show little compositional variability. All contained sub-angular to well-rounded sand grains that ranged from medium silts to very coarse sands (based on measuring the smallest and largest sand grains in each slide), frequent diatoms/sponge spicules, and a fine-grained, brown siliceous amorphous matrix. The main variation across the sedimentary sequences is in the grain to matrix ratio.

The lower two thin-sections from Unit 1, which comprise loosely consolidated sandy-silt diatomite, have no evidence of structure and contain the most densely packed quartz grains (~33% cover). The thin-sections in all following units are densely packed with quartz grains (~25–33% cover) but contain bands or patches where the density of quartz grains is much less (~5–10% cover). There is no evidence of iron-staining except for the lowermost thin-section from Unit 1 and Unit 4. Organic material is rare, with occasional amorphous organic materials in some thin-sections (though showing no trend throughout the sequence) and a single section with rare evidence of organics with cellular preservation.





close proximity to each other in the field (~10 m) and their stratigraphic relationship was easily traced. All footprints are located on the top of the first section but beneath the second section.



Figure 3. Representative photo-micrographs in cross-polarised light of Alathar palaeolake sediments. A) 3–5 cm from Unit 2. B) 130–132 cm from Unit 4b. C) ~146 cm from unit 5. D) 177–181 cm from Unit 7. The key thing to note between these representative samples is the similarity. There is a constant input of allogenic coarse-sand to medium-silt grains throughout the sequence, whilst the matrix is always brown amorphous silica.

OSL dating

Samples for optically stimulated luminescence (OSL) dating were taken from sediments directly below (Unit 3; PD61) and above (Unit 5; PD62) the footprint bearing unit and yielded ages of 121 ± 10 and 112 ± 9 ka, respectively, effectively bracketing the age of the prints (Table 1). An additional OSL sample was taken from the underlying aeolian sands (Unit 1; PD60) and dated to 255 ± 27 ka. The formation of the lake, therefore, can be constrained to the penultimate interglacial (i.e. MIS 5e) and importantly the footprints lie within the stratigraphic section as opposed to above it, again confirming the presence of fauna and hominins in this part of Arabia during a humid phase.

Sample	$\mathbf{D}_{\mathbf{b}}$	D _b (Gy)	OD (%)	Total dose	Age (ka)
	calculation			rate, D _r	
	method (n)			(Gy/ka)	
PD60	CAM (15)	11±1	33 ± 7	0.43 ± 0.01	255 ± 26
PD61	CAM (16)	115 ± 8	27 ± 5	0.92 ± 0.03	121 ± 10
PD62	CAM (32)	121 ± 8	39 ± 5	1.05 ± 0.04	112±9

Table 1. Summary dating results and ages.

Diatom analysis

Diatom assemblages from all three samples suggest oligotrophic (low nutrient availability) freshwater conditions, although there are subtle differences between them and hence inferred aquatic environments. The Unit 2 sample is dominated by benthic/littoral taxa, such as Nitzschia amphibia, Sellaphora pupula and Cymbella spp. though periphytic/tychoplanktonic taxa such as Staurosira constuens and varieties are also present. Some freshwater plankton are also present, notably Cyclotella (now Lindavia) ocellata and the more mesotrophic Aulacoseira granulata. The former is typical of oligotrophic lakes in Europe today across a range of lake depths, but also found in Ethiopian lakes at the start of Holocene filling (Loakes et al., 2018), while the latter is found in deep and well-mixed lakes but also more shallow and turbid systems. Benthic taxa more typical of higher conductivity are also found (e.g. Amphora copulata). This suggests the assemblage covers a range of lake conditions, but the site was always fairly shallow and fresh. The Unit 4b sample has a similar assemblage but L. ocellata is absent, while some valves of the aerophilous Hantzschia amphioxys were observed. Valve breakage is noticeably greater in this sample. Together, this suggests that the lake, though still fresh, had a lower water level in this period and perhaps occasional desiccation, resulting in more in wash from the catchment and greater turbulent mixing (leading to greater valve breakage). The Unit 7 sample has many of the same benthic taxa as the other samples but additionally includes *Aulacoseira ambigua* as well as *A. granulata* (both mesotrophic taxa). The freshwater facultative planktonic *Ulnaria acus* is also present in this sample.

Diatom-inferred conductivity for all samples suggest freshwater conditions in all cases. All samples also contain chrysophyte cysts, supporting an interpretation of freshwater and generally low/medium nutrient concentrations in all sections.

Depositional model

The interpretation provided by the diatom palaeoecology is supported by the sedimentary analysis. There are no evaporitic minerals present, with XRD demonstrating 90–100% quartz with the rest composed of K-feldspar, suggesting that the water body was unlikely to be brackish or saline. Likewise, the sediments suggest changes in lake extent and depth with clear evidence of episodic drying events. This is shown by horizontal bedding with laterally continuous sandy-silt diatomite interdigitated with laterally continuous sand layers. These characteristics are present in Units 2, 3, 4a, and 5. The sandy-silt diatomite is indicative of sedimentation during a wetter phase within a shallow freshwater lake. Sand beds were then deposited during arid phases when lake levels dropped, and the lakebed desiccated.

The presence of vegetation is evidenced by thin-elongate mottling in Units 2, 3, and 5, which typically result from local chemical and biological heterogeneities where organic matter has been oxidised (Collinson, 1996). Further evidence for vegetation is shown by the presence of root casts that run between the horizontally bedded diatomite layers in Unit 3. Vegetation growth may have been post-depositional or occurred during the deposition of these units. In the latter case, this would suggest a slow sedimentation rate and shallow waters, of which is consistent with the diatom palaeoecology from Alathar. Mottling and root casts are not present in Units 4a, 4b, 6, or 7 and indicate a reduction in vegetation at the site during the deposition of these units. This may reflect more turbulent and shallow conditions which inhibit aquatic plant growth (Talbot and Allen, 1996) and is consistent with the Unit 4b diatom assemblage.

A sparse and unstable vegetative environment surrounding the lake body is indicated by the constant influx of medium-silt to very-coarse allogenic sand grains throughout the sequence. Despite some variation in the grain to matrix ratio, all sections were predominately densely-packed with moderately to well-sorted sand grains (25–35% coverage) within a brown, amorphous matrix. This contrasts with the nearby site of Al Wusta, where allogenic sand- to silt-sized grains are rare which suggests enough vegetation was present to stabilise surficial sands surrounding the Al Wusta lake body (Groucutt et al., 2018). It is not clear whether the local vegetative environment surrounding Alathar was a consequence of local hydrological factors (Alathar is more elevated and situated further from the edge of the present-day dune field) or reflects different climatic conditions during its existence.

The final variation to note within the sequence is that the sediment varied in its level of cohesion. The sediment in Unit 2 was friable, whereas all other units were more consolidated. The variations in cohesion probably reflect differences in the grain to matrix ratio, with more consolidated sections containing a greater ratio of fine-grained matrix. The micro-facies analysis supports this view as two thin-sections from Unit 2 have the highest grain to matrix ratio, whereas thin-sections from all other units have areas that are more matrix dominated with only 5–10% sand cover (though still with areas of 25–33% densely packed sand grains). The greater grain to matrix ratio in Unit 2 probably reflects the fact that the surrounding landscape had not yet fully responded to the inception of a pluvial phase, with limited vegetation present to stabilise the surrounding dunes.

In summary, the Alathar sediments are interpreted as recording the presence of an oligotrophic/mesotrophic shallow freshwater lake that was subject to episodic desiccation. Based on the diatom and sedimentary analysis, it is not clear whether the lake was perennial and underwent rare desiccation events, or whether the lake was primarily rainfall fed and underwent frequent desiccation (perhaps seasonal). However, for the purposes of the present study the two most important observations are that: (1) the footprints lie within the lacustrine deposit and therefore demonstrate the presence of hominins in Arabia within a humid phase; and (2) the water body was fresh and therefore provided a vital resource for hominins and fauna in the western Nefud Desert, Saudi Arabia. Further research at the site, or of nearby similar palaeolake deposit, may elucidate the role, or lack thereof, seasonal fluctuations in humidity and precipitation played in regulating the Arabian lakes during the Pleistocene

Fossil and ichnofossil analysis

<u>Taphonomy</u>

In total, 233 fossils were collected and analysed (for results of the taphonomic analysis and full skeletal inventory see Tables 2 and 3, respectively). While most fossils were loose on the surface, a few were found eroding out of the palaeolake sediments and required shallow excavations for their retrieval (Fig. 6G). The assemblage is dominated by small fragments, most of which fall between 21–50 mm in length (n=142, 76%) and 11–30 mm in width (n=145, 78%). The abundance of small fossils, coupled with the fact

that no additional fossils were found in the days following this initial survey, suggests a comprehensive recovery of surface material at the site, although very small fossils are likely to still have been missed. Unweathered specimens are rare (n=4, 1.7%) and most can be assigned to weathering stages 1-3 (n=137, 58.8%) indicating a slow but eventual burial of bones. Black manganese stained bone (n=22, 12.7%) is consistent with deposition in damp sediments (Fernández-Jalvo and Andrews, 2016). A handful of specimens exhibit white bleaching (n=6, 3.5%) characteristic of abrasion by fine windblown sand, a process common in desert settings (Fernández-Jalvo and Andrews, 2016) including Arabia (see also *Chapter Six*). Furthermore, this suggests that the fossil assemblage, or part thereof, has been sub-aerially exposed for some time. Wind abrasion may also be responsible for the significant rounding noted on many of the specimens (n=24, 13.9%) and for some specimens there is a clear correlation between the bleaching and rounding. Green-fractured long bones are abundant (*n*=23, 40% of midshafts) and carnivores appear partly responsible, as evidenced by tooth marks on green-fractured bone. That said, tooth-marked specimens are scarce (n=6, n=6)4.0%). This may, however, be largely driven by adhering sediments (n=31, n=31)17.9%) and overall poor cortical surface preservation of many of the fossils. Long bones are characterised by shafts that retain less than half their original circumference (n=57, 79.2%) and this is probably the combined result of various pre- and post-depositional processes. Crushed specimens (n=18, n=18)13.1%) attest to the assemblage at some point being situated beneath a significant weight of sediment that has since eroded (e.g. lake sediments) or moved (e.g. dune migration).

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		Small	Medium	Large	Indet.	Total
		mam.	Mam.	mam.	mam.	-
Midshaft breakage						
Green	n	4	23	-	-	27
\mathbf{Dry}	n	1	12	-	1	14
Intermediate	n	2	15	-	1	18
Circ. completeness					-	-
Type 1	n	7	48	-	2	57
Type 2	n	-	3	-	-	3
Type 3	n	1	9	1	1	12
Weathering					-	-
0	n	1	1	-	2	4
1	n	1	31	-	3	35
2	n	2	48	-	6	56
3	n	3	34	1	8	46
4	n	-	5	-	1	6
Indet.	n	4	63	1	18	86
Crushing	n	1	14	-	3	18
	%	9.1%	11.3%	0.0%	8.3%	13.1%
Gnawing	n	-	7	-	-	7
_	%	0.0%	5.6%	0.0%	0.0%	4.0%
Abrasion/rounding	n	3	18	-	3	24
	%	27.3%	14.5%	0.0%	8.3%	13.9%
Bleaching	n	-	4	-	2	6
	%	0.0%	3.2%	0.0%	5.6%	3.5%
Manganese	n	2	18	-	2	22
staining	%	18.2%	14.5%	0.0%	5.6%	12.7%
Adhering sediment	n	1	26	-	4	31
	%	9.1%	21.0%	0.0%	11.1%	17.9%

Table 2. Results of the taphonomic analysis broken down by animal size class("%" values refer to the % of NISP).

	Small mammal	Medium mammal	Large mammal	Indet. mammal	Total
NRSP	11	182	2	38	233
NISP	11	124	2	36	173
Element NISP					
Horn core	-	3	-	-	3
Crania	-	7	-	-	7
Maxilla	1	-	-	-	1
Mandible	-	4	-	-	4
Isolated tooth	-	16	1	-	17
Atlas	-	1	-	-	1
Axis	-	1	-	-	1
Thor. Vert.	-	1	-	-	1
Indet. Vert.	-	1	-	-	1
Rib	-	4	-	-	4
Scapula	1	2	-	-	3
Pelvis	-	1	-	-	1
Humerus	1	5	-	-	6
- Prox. ep.	-	-	-	-	-
- Prox. ep. + shaft	-	-	-	-	-
- MSHF	1	3	-	-	4
- Dist. ep. + shaft	-	2	-	-	2
- Dist. ep.	-	-	-	-	-
Radius	1	2	-	-	3
- Prox. ep.	-	1	-	-	1
- Prox. ep. + shaft	-	1	-	-	1
- MSHF	1	-	-	-	1
- Dist. ep. + shaft	-	-	-	-	-
- Dist. ep.	-	-	-	-	-
Femur	-	1	-	-	1
- Prox. ep.	-	-	-	-	-
- Prox. ep. + shaft	-	-	-	-	-
- MSHF	-	-	-	-	-
- Dist. ep. + shaft	-	1	-	-	1
- Dist. ep.	-	-	-	-	-
Tibia	-	2	-	-	2
- Prox. ep.	-	-	-	-	-
- Prox. ep. + shaft	-	-	-	-	-
- MSHF	-	1	-	-	1
- Dist. ep. + shaft	-	-	-	-	-
- Dist. ep.	-	1	-	-	1

Table 3. Complete skeletal (NISP) inventory broken down by animal size

 class

	Small mammal	Medium mammal	Large mammal	Indet. mammal	Total
NRSP	11	182	2	38	233
NISP	11	124	2	36	173
Element NISP	-	-	-		-
Metatarsal	-	3	-	-	3
- Prox. ep.	-	2	-	-	2
- Prox. ep. + shaft	-	1	-	-	1
- MSHF	-	-	-	-	-
- Dist. ep. + shaft	-	-	-	-	-
- Dist. ep.	-	-	-	-	-
Metapodial	1	9	-	-	10
- Prox. ep.	-	-	-	-	-
- Prox. ep. + shaft	-	-	-	-	-
- MSHF	1	4	-	-	5
- Dist. ep. + shaft	-	4	-	-	4
- Dist. ep	-	1	-	-	1
Phalanx	-	3	1	-	4
Midshaft frag.	6	58	-	2	66
Unidentified	-	58	-	36	94

Table 3. Continued.

Systematic palaeontology

Order **Proboscidea** Iliger, 1811 Family **Elephantidae** Linnaeus, 1758 Elephantidae sp.

Description. – Two large enamel fragments (WNEF17_1/217, 230) are consistent with elephantids, but the fragments are small and poorly preserved and provide no further taxonomic insight.

Order *Artiodactyla* Owen, 1848 Family *Bovidae* Gray, 1921 Genus *Oryx* de Blainvill, 1816 *Oryx* sp. Description and remarks. – Numerous teeth and tooth fragments resemble those of *Oryx*, with upper molars and premolars having a simple occlusal profile and U-shaped infundibulum. A fragmented upper molar (WNEF17_1/198, 235 [refits]) exhibits a basal pillar that juts lingually before joining the protocone (or metaconule), with the enamel between the two creating a thin oval slit that most closely matches that seen on the second and third upper molars of *O. gazella*, albeit similar features can also occur in other *Oryx* species. An additional poorly preserved upper molar (WNEF17_1/142) is similar in overall appearance and probably represents the same taxon. A partial horn core and parietal bone (WNEF171/218) may also be *Oryx*, but the specimen is distorted and how much of the medio-lateral compression of the horn core is a result of this is difficult to discern.

The extant endemic *O. leucoryx* was abundant in Arabia until relatively recently (Uerpmann, 1987) and *Oryx* fossil remains have been reported from the middle (Thomas et al., 1998; Stimpson et al., 2016; Stewart et al., 2019) and late Pleistocene (McClure, 1984) of Arabia suggesting a long-standing presence in the region. The specimens described here, and possibly much of the medium-sized mammalian post-cranial material recovered from the site, can probably be referred to *Oryx*.

Small Bovidae gen. et sp. indet.

Description. – Two small bovid metapodial shaft fragments (WNEF17_1/22, 119) represent at least one other smaller bovid at the site.

cf. large Bovidae gen et sp. indet.

Description. – A large proximal (or intermediate) phalanx, preserving the distal epiphysis and diaphysis, is provisionally referred to a large Bovidae. The specimen is poorly preserved, exhibits significant cortical exfoliation and exposure of cancellous bone, and is slightly distorted.

Taxon	Fossil	Ichnofossil
		(prints)
Elephantidae sp.	х	
Proboscipeda isp. (Palaeoloxodon sp.)		Х
Hippipeda isp. (Equus sp.)		х
<i>Oryx</i> sp.	х	
Lamaichnum isp. (Camelus sp.)		Х
Bijugopeda isp. (Pelorovis antiquus).		Х
cf. Pecoripeda isp. (medium-sized bovid)		Х
Small bovid gen. et sp. indet	Х	
cf. large bovid gen. et sp. indet	Х	
Hominipes modernus (Homo sapiens)		х

Table 4. Fossil and ichnofossil taxa identified Alathar (possible trackmakers)

are listed in parentheses)

Systematic ichnology

Ichnogenus *Proboscipeda* Panin and Avram, 1962

Proboscipeda isp.

Description. – Large circular to near-circular tracks (n=44), preserved as concave epirelief impressions in the palaeolake sediment, are clearly attributable to a proboscidean (Fig. 6D, E). Tracks are typically longer than they are wide, but some have a width equal to length. Track length varies greatly, with diameters ranging from 190–630 mm, indicating the presence of a herd consisting of both adults and juveniles. Displacement rims and radial fractures (following Pasenko, 2017) were common and often encompassed the track. Toe impressions and overprinting were rarely observed. Load deformation was clearly visible in one of the prints where the palaeolake sediment had broken off, exposing the print cross-section.

Remarks. – The lack of toe impressions and length greater than width is consistent with *Pro. enigmatica*, the type ichnospecies for the ichnogenus *Probosciepda* (Panin and Avram, 1962). The Alathar prints are, however, significantly larger than the range reported for *Pro. enigmatica* (420–520 325 mm) and are more comparable in size to prints from Wally's Beach in Canada, attributed to *Pro. panfamilia* (McNeil et al., 2007). However, *Pro. Panfamilia* often exhibit toe impressions and forefoot overprinting (McNeil et al., 2007; Neto de Carvalho, 2009; Neto de Carvalho et al., 2016), features which are absent in the Alathar tracks. It's possible, however, that wind abrasion has removed some features, including toe impressions. The Alathar tracks are therefore referred to the ichnogenus *Proboscipeda*.

Proboscidean tracks are relatively common and widespread in the Mio-Plio-Pleistocene ichnofossil record (e.g. McNeil et al., 2007; Robert. 2008; Neto de Carvalho, 2009; Bibi et al., 2012; Neto de Carvalho et al., 2016). *Palaeoloxodon antiquus, Mammuthus primigenius, Elephas Cypriotes*, among others, have all been proposed as probable trackmakers, with researchers drawing on print morphometric data, associated body fossils, and proboscidean palaeobiogeography. The large Alathar track lengths far exceed those of the extant African *Loxodonta africana* (170–530 mm, n=30) and Asian *Elephas maximus* (370–400 mm, n=2). The extant African elephants may also be discounted as possible trackmakers on the basis of their late Pleistocene fossil record, which, like their present-day distribution, is restricted to sub-Saharan Africa (Sanders et al., 2010).

During the late Pleistocene, proboscideans were far more diverse and widespread, and many species far exceeded the size of the extant elephants. The large grassland-adapted *Pal. iolensis*, considered by some to represent the terminal subspecies of the *Pal. recki* lineage, may have persisted in North Africa until c. 35 ka (Coppens et al., 1978; Sanders et al., 2010). Various large proboscideans (e.g. *Pal. antiquus, Mammuthus primigenius*) occupied parts of Europe up until the end of the late Pleistocene/early Holocene, but their ranges appear to have been restricted to the more northerly latitudes (Stuart, 2005; Pushkina, 2007). Proboscidean remains are notably scarce in southwest Asia from c. 400 ka onwards, possibly due to an increase in hominin hunting pressures in the region (Ben-Dor et al., 2011). Therefore, the findings presented here are of considerable interest. *Palaeoloxodon antiquus* remains recovered from Holon, Israel, may date to as young as c. 200 ka (Porat, 2007), but other researchers have questioned the validity of these dates, suggesting that fossil remains are in fact much older (c. 500 ka) (Bar-Yosef and Belmaker, 2011; Ben-Dor et al., 2011). More recently, remains tentatively attributed to *Pal. recki* were discovered at Shishan Marsh, Jordan, and dated to c. 266–125 ka (Pokines et al., 2018). Unstratified remains of *E.* sp. cf. *E. hysudricus* were also discovered at the site and probably originate from layers dated to c. 266–125 ka (Pokines et al., 2018). Other provisionally identified remains of *E. hysudricus* were also discovered at the nearby sites of Ma'ayan Baruch and 'Ain Soda, Israel, and dated to c. 500–220 ka (Lister et al., 2013). While it remains difficult to speculate as to the trackmaker, it seems likely that it was a large-bodied grassland adapted elephant (e.g. *P. recki*).

Ichnogenus *Hippipeda* Vyalov, 1965 *Hippipeda* isp.

Description. – A single digit impression (digit III) with a hemi-ellipsoidal/arrowhead outline that is tapered to the anterior (WNEF17_1/PR158; Fig. 6I). The track is widest towards the posterior and the margins of the posterior end of the track run roughly parallel. The two posterior bars connect and isolate the sole (following McNeil et al., 2007). Greatest length and width are 70 mm and 60 mm, respectively.

Remarks. – The Alathar print closely resembles those attributed to *Hip. cardstoni* from Walley's beach in Canada but is shorter than the range reported for this ichnospecies (90–120 mm) (McNeil et al., 2007). Given that only a single print is present at Alathar, it is referred to the ichnogenus *Hippipeda*.

Equids are relatively abundant in the Arabian Pleistocene fossil record (*Chapter Two*; Stewart et al., 2017). Remains of *E. hemionus* have been recovered from Ti's al Ghadah in the western Nefud Desert (Stimpson et al., 2016) and provisionally assigned remains from southern Arabia (McClure, 1984; Delagnes et al., 2012). Remains of an additional, larger equid were also found at Ti's al Ghadah (Stimpson et al., 2016), as well as at the late Pleistocene site of Khall Amayshan-4 (*Chapter Six*). The size of the Alathar track falls below those reported for African zebra in tracking guides (c.f. Stuart, 2013; Liebenberg, 2014), suggesting perhaps one of the smaller wild asses (e.g. *E. hemionus*), although it's possible that the trackmaker was a juvenile, or that the track size has been reduced due to wind abrasion.

Ichnogenus *Lamaichnum* Aramayo and Branco, 1987 *Lamaichnum* isp.

Description. – Bidigital, digitigrade tracks with rounded anterior ends and lacking claws (n=107). Anterior digits rarely convergent and are typically parallel. Posterior end wider than anterior and particularly so for forefoot. Hindfoot tracks ovoid in outline (Fig. 6H), whereas forefoot tracks are more triangular/heart-shaped, tapering to the anterior (Fig. 6G). Both forefoot and hindfoot impressions exhibit a posterior gap and a medial pocket was occasionally observed (following McNeil et al., 2007, Fig. 9). Tracks vary in length from 80–240 mm, indicating the presence of both juveniles and adults.

Remarks. – Broadly, the shape and size of the Alathar prints resembles L. sarjeanti but differ in that the length typically exceeds the width, whereas in L. sarjeanti the length and width are approximately equal (McNeil et al.,
2007). In this regard, the Alathar prints are more similar to *L. macropodum*, but lack claw marks often associated with this ichnospecies (Sarjeant and Reynolds, 1999; McNeil et al., 2007). Again, this may be the result of wind abrasion.

The Pleistocene camelid fossil record of Africa and Eurasia is scant, and most fossils are too poorly preserved to be adequately described (Harris et al., 2010). As a result, our understanding of the biogeographical history of *Camelus* remains patchy and the relationship between identified species unclear. In Arabia, remains of a large *Camelus* were recovered from the western Nefud Desert and dated to c. 500 ka (Thomas et al., 1998; Stimpson et al., 2016) and rock art depictions indicate the presence of wild camels in the region during the early Holocene (Guagnin et al., 2018). Given camels are well-suited to arid environments, it's possible that they have had a long-standing presence in the Arabian Peninsula from as early as the middle Pleistocene, and perhaps even earlier, making speculation about the trackmaker of the Alathar prints difficult.

Ichnogenus *Bijugopeda* Sarjeant and Reynolds, 1999 *Bijugopeda* isp.

Description. – A single large bidigital, digitigrade footprint with two separate kidney bean-shaped toe impressions is clearly that of a large bovid (WNEF17_1/070; Fig. 6H). The anterior and posterior ends taper inwards producing a medial pocket that is widest in the centre of the track. Greatest length and width measure 140 mm and 190 mm, respectively. The greater width, coupled with the tapered anterior and posterior ends, produces a track that is oval in outline. Another large, ovoid track with a broadly similar outline may represent a second track but it is too poorly preserved to be certain. Remarks. – The shape and size of the Alathar track closely matches those attributed to *Bijugopeda anterofossa* from Walley's Beach in Canada suggested to have been produced by the large extinct *Bison antiquus* (McNeil et al., 2007). It differs in its overall shape, as well as in its much greater length and width, to tracks produced by alcelaphines (e.g. *Alcelaphus*) and hippotragines (e.g. *Oryx*), as displayed in various tracking guides (e.g. Stuart, 2013; Liebenberg, 2014). Considering this, and the fact that *Pelorovis* is the only large-sized bovid (size class IV; Bunn, 1982) known from the western Nefud Desert during the Pleistocene (*Chapter* Six; Thomas et al., 1998; Groucutt et al., 2018), it seems reasonable to suggest that *Pelorovis* is the likely trackmaker at Alathar.



Figure 4. Bijugopeda sp. track (WNEF17_1/070).

Ichnogenus *Pecoripeda* Vyalov, 1965 cf. *Pecoripeda* isp.

Description. – A medium-sized bidigital, digitigrade track (WNEF17_1/205; Fig. 6G) with convex lateral margins giving the track and ovoid outline. Length and width measured 60 mm and 70 mm, respectively, 330 with the widest point of the track being across its centre. Track exhibits claw impressions, as well as shallow posterior and anterior gaps, but lacks a medial pocket. A second similar, albeit slightly distorted, print was found adjacent to this print and probably represents the same individual (WNEF17_1/204). Given the relative positions of the prints, the individual appears to have been stationary.

Remarks. – The Alathar tracks differ from most *Pecoripeda* tracks in their oval outline and being wider at the middle, as opposed to the heel (see Lucas, 2007). In this latter feature they resemble *Pecoripeda djali* but differ again in being wider than they are long and with less discernible toe impressions. The Alathar tracks are tentatively referred to the ichnogenus *Pecoripeda*, but do not resemble, to the best of my knowledge, any described *Pecoripeda* ichnospecies. It's possible that wind abrasion has drastically altered the morphology of the print. Indeed, Wiseman and Groote (2018) found tide action significantly and rapidly altered the morphology of ungulate tracks following exposure (see also Zimmer et al., 2018). For example, they found that the borders of some ungulate prints went from being undercut at the start of the experiment to being shallow and slanted within just four days. 120 thousand-year-old footprints



Figure 5. Example of a cf. Pecoripeda sp. track (WNEF17_1/205).

Ichnogenus *Hominipes* Kim et al., 2008 *Hominipes modernus* Kim et al., 2008

Description. – plantigrade tracks with a pronounced medial longitudinal arch, abducted hallux, rounded digit and heel impressions, and a wide metatarsal region (n=7). In some cases, the heel, medial metatarsal heads, and hallux are most strongly impressed, reflecting medial weight transfer during bipedal locomotion. Length (Heel-D2) and ball width (B1-B2) ranged from 247–292 mm and 100–130 mm, respectively.

Remarks. – to date, only two hominin ichnotaxa have been formally described – *Praehominipes laetoliensis* (Meldrum et al., 2011) and *Hominipes modernus* (Kim et al., 2008). The Alathar tracks clearly differ from those of *P. laetoliensis* (based and named after the Laetoli trackways) in their large size and differences in morphology, in particular their rounded heel, prominent and well-defined ball and instep regions, and fixed longitudinal arch. The Alathar prints are consistent in both size and morphology with Hominipes modernus and for reasons discussed below it is argued that Homo sapiens was the probable trackmaker.

Hominin and fauna tracks

A total of 376 tracks were recorded of which 170 could be either confidently or provisionally referred to an ichnotaxon. Tracks exhibit similar states of preservation and most are quite shallow resulting from wind erosion following exhumation, the extent of which is highlighted by significant erosion of the overlying Section 2. Trampling is most severe in the centre and towards the southern end of the deposit and overprinting is common, making identification of trackways difficult.

Seven hominin prints were identified (Fig. 7). An additional four prints (PR280, PR236, PR366, PR282) are provisionally referred to hominins as they are of a consistent size and shape, but lack fine details required for positive identification. Four prints (HPR001–004) were found adjacent to one another along the southwestern edge of the palaeolake exposure (Fig. 1), and given their similar orientation, distances from one another, and differences in size (Table 6), they are interpreted as two, or up to three, individuals travelling together. Mean print length is closest to that of modern unshod Daasanach people (difference $[\Delta] = 0.8$ cm), whereas the mean print breadth is most similar to the single Vârtop Cave print ($\Delta = 1.0$). The Alathar prints are comparatively broad with a footprint index (FPI) closest to the Valsequillo (Δ = 0.02) and Rocammofina (Δ = 0.03) prints. It is worth noting, however, that footprint morphometry can vary significantly within a single species (for example, see Dingwall et al., 2013, Shu et al., 2015) and even within an individual trackway (Morse et al., 2013). Furthermore, it has been shown that post-exhumation degradation (e.g. weathering, tide action) can significantly alter the morphology and size of hominin tracks (Wiseman and Groote, 2018; 333 Zimmer et al., 2018). Wiseman and Groote (2018) found an increase in footprint length of as much as 6% as a result of lake tides acting on the tracks. It has also been suggested that wind erosion, too, can significantly alter track shape and appearance (Zimmer et al., 2018). Therefore, it seems possible that wind abrasion has altered the Alathar track assemblage in some form or another, and any extrapolations based on footprint size or morphology should bear this in mind. Still, we present stature and mass estimate below.

Speed estimates obtained for the only identifiable stride in the Alathar assemblage (i.e. HPR001 and HPR003) returned values around the expected transition from walking to running (~2.2 m/s) (Dingwall et al. 2013; Bennett and Morse, 2014). Therefore, the "walk and run" regression equation was selected to estimate stature (eqn 2) and body mass (eqn 3) of the Alathar printmakers, with results reported in Table 5.

Stature_{walk & run} =
$$73.29 + 3.78*$$
FPL ± 5.4 [2]

$$Mass_{walk \& run} = 3.94 + 1.87*FPL \pm 3.70$$
 [3]

Stature estimates for the Alathar hominins ranged from 166-182 cm with a mean (170 cm) closest to that of the Daasanach and estimates for early *H. sapiens* (Table 7; Fig. 9). Mass estimates ranged from 53-57 kg with a mean (53 kg) falling between the Daasanach, early *H. sapiens*, and *H. neanderthalensis*. Discriminant function values (*D*) for three of the prints (i.e. HPR002, HPR004, HPR001+HPR003) predicted that all three were produced by males, while insufficient data precluded sex predication analysis for other hominin tracks.

120 thousand-year-old footprints



Figure 6. A) Plan view of the Alathar palaeolake deposit, researchers indicated by arrows; (B) first section (Units 1-4); (C) second section (Units 5-7) overlying the first but located towards the centre of the palaeolake; (D, E) examples of elephant tracks, *Proboscipeda* isp.; (F) camelid trackway, *Lamaichnum* isp.; (G, H) examples of camelid forefoot (G) and hindfoot (H) tracks, *Lamaichnum* isp.; I) equid track, *Hippipeda* isp.; (J) bovid axis vertebrae eroding out of the palaeolake sediment.

120 thousand-year-old footprints



Figure 7. A) Footprint morphometric data collected in this study (image taken and modified from Bennett et al. [2009]); B-G) examples of hominin footprints. T, B, I, and H denote toe margin, ball, instep, and heel, respectively.

Table 5. Stature, mass, and speed estimates for the Alathar prints using the walk and run linear fit equations from Dingwall et al. (2013).

Print	Stature (cm)	Mass (kg)	Speed (m/s)
HPR001 + HPR003	181.78	57.61	2.99
HPR002	166.28	49.94	-
HPR004	173.46	53.50	-
HPR005	167.03	52.82	-
PR212	-	-	-
PR347	163.63	53.4	-

Track	Side	Heel-	Heel-	Heel-	Heel-	Heel-	B1-B2	H1-H2	I1-I2	Toe
		Hallux	D2	D3	D 4	$\mathbf{D5}$				traces
HPR001	R	28.8	29.2	28.9	28.7	27.8	13.0	7.0	6.0	I, II, III?
HPR002	R	24.6	25	24	22	21.5	13.0	5.8	7.0	-
HPR003	R	28.6	29	-	-	-	12.0	7.5	5.5	I?
HPR004	R	26.5	27	25.5	24	22	10.0	6.5	5.5	-
HPR005	\mathbf{L}	24.8	25.8	-	-	-	10.5	6.6	-	-
PR212	R	-	-	22.8	22.3	20.8	-	5.4	-	III, IV, V
PR347	\mathbf{L}	23.9	24.7	-	-	-	11.1	5.9	3.8	II?

Table 6. Alathar footprint morphometric data (cm) for the seven confidently identified hominin prints

Table 7. Footprint length, breadth, and index values compared to those of modern humans and various fossil hominin track assemblages. Taxa listed in parentheses are suspected trackmakers.

Site	Footprint length (cm)		Footprint breadth (cm)		FPI	Reference
	Mean	Range (s.d.)	Mean	Range (s.d.)		
Modern Human (Daasanach)	25.4 (<i>n</i> =41)	20.0 - 29.5 (2.1)	9.7 (<i>n</i> =41)	7.4 – 11.8 (0.9)	0.38	Dingwall et al., 2013
Valsequillo (H. sapiens)	21.0 (<i>n</i> =?)	13 – 31 (?)	9.4 (<i>n</i> =?)	7.0 – 13.0 (?)	0.46	González et al., 2006
Walvis Bay (Hol. H. sapiens)	22.8 (<i>n</i> =87)	$19.6 - 26.1 \ (1.7)$	8.7 (<i>n</i> =83)	$5.0 - 11.0 \ (0.9)$	0.38	Morse et al., 2013
Vârtop Cave (H. neanderthalensis)	22 (n=1)	-	10.6 (<i>n</i> =1)	-	0.48	Onac et al., 2005
Roccamonfina (H. heidelbergensis)	24 (<i>n</i> =56)	-	10 (<i>n</i> =56)	-	0.41	Arvanzini et al., 2008
Happisburgh (H. antecessor)	19.1 (<i>n</i> =12)	14.0 - 26.0 (4.2)	7.5 (<i>n</i> =12)	5.0 - 11.0 (1.8)	0.39	Ashton et al., 2014
Ileret (H. erectus)	25.3 (<i>n</i> =28)	20.5 - 30.5 (2.2)	9.6 (<i>n</i> =36)	7.5 - 12.7 (1.2)	0.38	Hatala et al., 2017
Alathar (Pleist. H. sapiens)	26.2 (n=6)	23.9 - 28.8 (2.1)	11.6 (n=6)	10.0 - 13.0 (1.2)	0.44	



Figure 8. Hominin print digital elevation models (DEM).



Figure 9. A) Stature estimates of Alathar printmakers compared to known and estimated statures of modern humans, early *H. sapiens*, and *H. neanderthalensis*; B) mass estimates; C) stature and mass scatterplot; and D) directional movement patterns of hominin (left) and non-hominin herbivore (right) tracks.

Lamaichnum (camelid) and Proboscipeda (elephant) tracks are most abundant, whereas other non-hominin ichnotaxa are represented by only a handful of specimens. The identification of elephant trackways was made easier by their large size, and tracks clearly belonging to adults, subadults, and juveniles document a herd moving through the landscape (Figs. 1 and 6). A Rayleigh's test for directionality revealed that elephant tracks are non-randomly orientated (Fig. 9) (Rayleigh's R = 0.369, p = 0.001; Watsons U^2 = 1.467, p < 0.005), with elephants moving in a mostly southward direction. This is consistent with travel towards or around the lake, which, based on sedimentological data, lied southwest of the present-day palaeolake deposit. Likewise, the wide range of camelid print sizes indicates the presence of both adults and juveniles, but in contrast the elephant tracks are randomly orientated (Rayleigh's R = 0.142, p = 0.137; Watsons $U^2 = 0.106$, p < 0.005). A test including all tracks (hominin and non-hominin) also found tracks to be randomly orientated (Rayleigh's R = 0.061, p = 0.393; Watsons $U^2 = 0.338$, p < 0.005), suggesting movement in the vicinity of the lake was not geographically constrained. That said, there is a general north-south trend in track orientation (Fig. 9) that might reflect some perpendicular movement towards and away from the lake. This trend may also reflect movements tied to seasonal shifts in rainfall and north-south seasonal movements following lakes have been observed among modern elephant populations in East Africa (Thouless, 1995). The small sample size of the hominin prints precluded testing for directionality, but two points are worth noting: (1) hominin prints are scattered across the palaeolake and orientated in various directions (Figs. 1 and 9); and (2) the group of two or three hominins travelling together are, like the elephant herd, travelling south.

Stable carbon and oxygen isotope analysis

Bulk δ^{13} C and δ^{18} O measurements of the fauna analyzed in this study are shown in Figure 10 (see also Appendix B, Table S4). δ^{13} C results from the Bovidae samples (range = -0.3 to -4.8‰) imply significant proportions of C₄ biomass in their diets. However, unlike recently published isotope work from fossil fauna at the middle Pleistocene site of Ti's al Ghadah (*Chapter Three*; Roberts et al., 2018) there also appears to be a significant contribution of C₃ vegetation. A similar scenario exists for the bulk measurement of the extinct elephant at Alathar (δ^{13} C = -1.8‰) that again shows a strong reliance on C₄ graze but not as strong as seen among *Palaeoloxodon* at Ti's al Ghadah (*Chapter Three*; Roberts et al., 2018).

The sequential δ^{13} C data from the elephant demonstrates a relatively persistent source of vegetation throughout the formation of the tooth, apparently primarily C₄ graze but with some contributions of C₃ grasses, sedges, and/or browse (Appendix B, Fig. S3, Table S5). The sequential δ^{18} O fails to document any clear seasonal variation in water source or environmental stress, though some fluctuations towards higher values (and potentially higher aridity) are present. Overall, the elephant specimen demonstrates very little variation in either δ^{13} C or δ^{18} O, suggesting reliable access to stable water bodies and similar types of vegetation on an intra- and inter-annual basis, perhaps maintained by long-distance seasonal migrations.



Figure 10. Stable carbon (δ^{13} C) and oxygen (δ^{18} O) isotope values and information relating to the fossil samples analysed in this study. Data for Ti's al Ghadah from *Chapter Three*.

DISCUSSION

The hominin and non-hominin mammal footprints reported here, coupled with the sedimentological, fossil, and isotopic data, provide a unique opportunity to investigate the interplay between late Pleistocene hominins, their immediate ecology, and associated fauna within the Arabia interior. Alathar represents a shallow freshwater lake that would have provided a vital resource and habitable landscape for hominins and fauna within the western Nefud Desert during the penultimate interglacial (MIS 5e). The freshwater nature of the lake is consistent with other nearby lacustrine deposits dated to MIS 5, such as Al Wusta (Groucutt et al., 2018), Jebel Ghawtar (Parton et al., 2018), and sites 16.5 and 17.3 (Rosenberg et al., 2013). Alathar attracted a variety of medium and large mammals, as represented by abundant camel, elephant, bovid, equid, and hominin tracks and fossils. Heavy trampling of the Alathar palaeolake surface suggests dense aggregations of animals around the lake over the course of a few hours or days (cf. Roach et al., 2016). This may represent a dry period, during which herbivores congregate in large numbers around diminishing water supplies (Thrash et al., 1995; Valeix et al., 2010). This is consistent with the fragmented diatom assemblage associated with the footprint bearing unit and may also, in part, explain the heavily fragmented fossil assemblage. Increasing aridity is also supported by diatom and sedimentary analysis, and it is clear that the lake underwent repeated desiccation events that might be tied to seasonal fluctuations in rainfall. Indeed, geomorphological studies of nearby palaeolake deposits (Parton et al., 2018), climatic modelling (Jennings et al., 2015), and isotopic data (*Chapter Three*; Roberts et al., 2018) suggest a strong dichotomy between winter and summer rainfall regimes during pluvial phases in the Nefud Desert.

Sequential δ^{18} O analysis of elephant tooth document some fluctuations toward higher values that could represent brief periods of increased aridity, but overall these fluctuations are not particularly pronounced, and both δ^{18} O and δ^{13} C suggest reliable access to water and vegetation on an intra- and inter-annual basis. As suggested in *Chapter Three* (Roberts et al., 2018), elephants may have maintained reliable access to resources by undertaking long distance migrations, as seen in modern-day elephant populations (Cerling et al., 2006). This is in line with previous findings that suggest the Nefud Desert was part of a larger interconnected system of palaeo-lakes and -rivers that linked the Arabian interior to the Near East and North Africa during the Pleistocene pluvial periods (Breeze et al., 2016). δ^{13} C values document abundant C₄ grasses in the diets of herbivores, but with a greater C₃ component than at Ti's al Ghadah (*Chapter Three*; Roberts et al., 2018). This could indicate different feeding habits of the bovids analysed here, wetter conditions promoting C₃ shrub and sedge growth, or winter rainfall supporting C_3 grasses. This is broadly consistent with various palaeoenvironmental proxies that indicate that the penultimate interglacial was particularly wet (Drake et al., 2013; Rosenberg et al., 2013; Jennings et al., 2015; Parton et al., 2015). The presence of elephants and *Oryx* at Alathar, and inferred presence of *Equus, Camelus*, and *Pelorovis*, is consistent with a well-watered semi-arid open grassland setting.

Tracks are orientated in all directions and suggest that animal movements were not geographically constrained, probably reflecting an open habitat. Elephant tracks document at least one herd travelling southward towards the lake and there is a general north-south trend among animal tracks that may reflect animal movements to and from the lake, or perhaps southerly migrations following the monsoonal rains as they retreated southwards during the dry season. Observations of watering holes in East Africa found bovids typically moved perpendicular to the lakeshore (that is, from the surrounding grasslands to the lakeshore to drink and forage, and back again) (Roach et al., 2016). In contrast, carnivores typically travel along lakeshores (Roach et al., 2016), a behaviour thought to increase hunting and scavenging success in arid environments where herbivores congregate around watering holes (Thrash et al., 1995; Redfern et al., 1995). Herbivore movement at Alathar is therefore consistent with drinking and foraging behaviour. The aggregation of herbivores would have made Alathar, and other freshwater lakes like it in the western Nefud Desert (e.g. Al Wusta; Groucutt et al., 2018), particularly attractive places for carnivores, and the presence of carnivores is evidenced by tooth-marked bones.

Likewise, Alathar may have been an attractive hunting ground for hominins, or as a place to drink and forage for plant foods. All prints are consistent in size with adults and the cluster of prints along the southwestern margin are interpreted as a group of two, or up to three, possibly adult males

travelling together in a southerly direction. At the very least these represent individuals who co-existed and moved across the same landscape within a short window, probably the same day. Assuming that the track assemblage represents a single group at a particular point in time, the random orientation of the tracks suggests that these hominins were not simply traversing the lake but were engaged in non-directional activities, perhaps foraging. There is no evidence of butchery at the site, nor were lithic artefacts recovered. This contrasts with numerous other MIS 5 palaeolake sites in the western Nefud Desert which document repeated visits to, and stone tool preparation within, lake margin habitats (e.g. Petraglia et al., 2011, 2012; Scerri et al., 2015; Breeze et al., 2017). Therefore, it seems that the Alathar lake served, at least on this occasion, as a place to drink and/or forage for plant foods. Importantly, the site demonstrates a spatial and temporal association between hominin and herbivore movement and landscape use patterns. Hominins and medium/large herbivores were occupying the same spaces and utilising similar resources (water and/or lakeside vegetation) at roughly similar times, probably within hours of one another. Lakes and rivers may have also provided corridors for long distance travel and migration (Boivin et al., 2013; Breeze et al., 2016; Roach et al., 2016) and archaeological data suggests that late Pleistocene hominins in Arabia were highly mobile and penetrated deeper into the dune fields than their middle Pleistocene predecessors (Scerri et al., 2015; Breeze et al., 2017).

Both *H. sapiens* and *H. neanderthalensis* are known from the immediately adjacent Levant during the late Pleistocene but seem to have occupied the region at different times (Shea, 2008). Respectively, their occupation appears to have been tied to regional climate fluctuations; *H. sapiens* was present when it was humid and warm, whereas *H. neanderthalensis* was present when it was arid and cold. *Homo sapiens*

appeared in the Levant during the warm penultimate interglacial, as represented by the dozens of individuals recovered from Skhul and Qafzeh (Grün et al., 2005), and an earlier dispersal is now suggested by the recent findings from Misliya Cave (Hershkovitz et al., 2018; but see Sharp and Paces, 2018). Homo sapiens also dispersed into Arabia during marine isotope stage 5 (MIS 5; 130–80 ka). Groucutt and colleagues (2018) recently reported a *H. sapiens* fossil finger bone dated to *c.* 90 ka from Al Wusta, a site just 11 km's south of Alathar. Numerous Middle Palaeolithic (MP) stone tool assemblages, some of which have been provisionally attributed to H. sapiens based on similarities with other Levantine and African MIS 5 toolkits, have also been recovered from the western Nefud Desert (Petraglia et al., 2012; Scerri et al., 2015), as well as further east and south (Armitage et al., 2011; Groucutt et al., 2015). As such, it appears that *H. sapiens* may have been geographically widespread in Arabia during MIS 5. In contrast, H. *neanderthalensis* is notably absent from the Levant during MIS 5 and only appears alongside the arrival of the cold and arid MIS 4 (Shea, 2008). The Tabun 1 H. neanderthalensis individual – excavated nearly 100 years ago – is the one possible exception to this pattern, but its precise provenance remains unknown (Garrod and Bate, 1937; Bar-Yosef and Callander, 1999), radiometric dating results have varied widely (Grün and Stringer, 2000; Mercier and Valladas, 2003), and the taxonomy of some of the fossils continues to be debated (Harvati and Lopez, 2017, and references therein). The apparent absence of *H. neanderthalensis* from the region during MIS 5 and semi-arid open grassland setting of the Nefud Desert during the penultimate interglacial points to *H. sapiens* as the likely trackmaker at Alathar. Track size, too, is most consistent with H. sapiens being the trackmaker, but how much the size and shape of these prints has been altered by processes such as wind erosion remains unknown, and, therefore, any interpolations from the track data should be considered speculative at best.

Interestingly, the Alathar hominin tracks document an arrival into the Arabian interior contemporaneous with the earliest securely dated arrival of H. sapiens outside Africa, as represented by the Skhul fossils (Grün et al., 2005). The findings presented here suggest that this early out of Africa dispersal radiated further than often considered (see also Armitage et al., 2011). Interglacial climatic amelioration of the Saharo-Arabian belt and coincidental trans-Saharan dispersal of African grassland taxa (Thomas et al., 1998; Drake et al., 2011; Drake and Blench, 2017; Groucutt et al., 2018) would have provided a relatively straightforward passageway for H. sapiens from Africa to Arabia via the Sinai Peninsula that did not require passing through the Levantine woodlands. The tracks and associated palaeoclimate data presented here provide a truly unique look into the immediate ecology of H. sapiens in the Arabian interior.

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APPENDIX

Appendix A. Optically stimulated luminescence (OSL) dating

Table S1. Age variations for each sample depending on oversaturation rejection criteria (see SI Text 3 for full discussion).

Sample	Oversaturation rejection criteria	Age (ka)
PD60	1	267 ± 16
	2	255 ± 26
	3	224 ± 14
PD61	1	128 ± 8
	2	121 ± 10
	3	118±8
PD62	1	115 ± 7
	2	112 ± 9
	3	99.3 ± 6.1

Table S2. The number of single aliquots which were measured, rejected after application of the criteria outlined in Table S1 and accepted for inclusion in the calculation of D_{b} . Samples indicated (DR) represent dose recovery data.

Sample	PD61	PD62	PD60	PD61	PD62		
	(DR)	(DR)					
Total number of a	liquots mea	sured					
	12	12	48	48	48		
Aliquots rejected	for the follou	ing reasons	-	-	-		
Poor recycling	1	0	1	0	1		
ratio							
Depletion by IR	7	2	29	29	11		
Recuperation	0	0	0	0	0		
Oversaturation	N/A	N/A	3	3	4		
Sum of rejected grains							
	8	2	34	31	16		
Acceptable individual D_e values							
	4	10	15	16	32		

Sample	Depth	Moisture	oisture Dose rate (Gy/ka)				
	below surface (m)	(%)	Beta	Gamma Cosmic		dose rate, (Gy/ka)	
PD60	$1.96{\pm}0.10$	5 ± 2.5	0.12 ± 0.01	0.17 ± 0.01	0.18 ± 0.02	0.44 ± 0.02	
PD61	1.02 ± 0.10	5 ± 2.5	0.49 ± 0.03	0.38 ± 0.02	0.20 ± 0.02	0.95 ± 0.04	
PD62	0.29 ± 0.10	5 ± 2.5	0.59 ± 0.04	0.38 ± 0.02	0.25 ± 0.02	1.08 ± 0.05	

Table S3. Sample depths, water content and dose rate

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Figure S1. Abanico plots displaying the normalised dose recovery data centred to unity for accepted aliquots with a preheating regime of 200°C held for 10 seconds prior to the measurement of the regenerated dose (L_x) and 160°C held for 5 seconds prior to the measurement of the test dose (T_x). See discussion in Supplementary

Text 3 for more details



Figure S2. Abanico plots displaying the spread of D_e values observed in samples PD60, PD61, and PD62 (left to right). The plot and two sigma errors are centred to the weighted mean, whilst the dark green line represents the CAM D_e value used for age estimation. Overdispersion values are shown in Table S5 and are discussed in Supplementary Text 3.

Appendix B. Results of stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) analysis

Table S4. Stable carbon and oxygen isotope values and information relating to the fossil samples analysed in this study. * Denotes specimens also sampled sequentially.

Sample ID	Tooth sampled	Taxa	δ ¹³ C(‰) (VPDB)	S.D.	δ ¹⁸ O(‰) (VPDB)	S.D.
WNEF17_1/143	P4	Oryx sp. cf. O. gazella	-4.8	0.1	1.4	0.1
WNEF17_1/111	Indet.	Bovidae	-3.0	0.1	-2.2	0.1
WNEF17_1/214	P4	Bovidae	-2.4	0.1	-0.6	0.1
WNEF17_1/198	M2	Oryx sp. cf. O. gazella	-3.4	0.1	0.0	0.1
WNEF17_1/188	Indet.	Bovidae	-0.8	0.1	0.3	0.1
WNEF17_1/275	Indet.	Bovidae	-1.7	0.1	-0.3	0.1
WNEF17_1/108	Indet.	Bovidae	-0.3	0.1	0.7	0.1
*WNEF17_1/217	Enamel	Elephantidae	-1.8	0.1	-3.6	0.1

Distance from root-enamel junction (mm)	δ ¹³ C (‰) (VPDB)	S.D.	δ ¹⁸ O (‰) (VPDB)	S.D.
0	0.4	0.1	-1.7	0.1
5	-0.8	0.1	-2.9	0.1
10	-1.1	0.1	-2.9	0.1
15	-0.5	0.1	-0.4	0.1
20	-0.5	0.1	-3.6	0.1
25	-0.7	0.1	-3.5	0.1
30	-0.2	0.1	-2.8	0.1
35	-0.3	0.1	-2.1	0.1
40	-1.2	0.1	-3.0	0.1
45	-1.2	0.1	-3.3	0.1
50	-0.4	0.1	-2.3	0.1
55	-1.2	0.1	-3.8	0.1
60	-0.8	0.1	-3.5	0.1
65	-0.9	0.1	-3.2	0.1
70	-1.5	0.1	-3.1	0.1
75	-1.6	0.1	-3.3	0.1
80	-0.2	0.1	-2.1	0.2
85	-0.8	0.1	-3.2	0.1
90	-0.8	0.1	-3.6	0.1
95	-0.8	0.1	-3.3	0.1
100	-2.3	0.1	-4.0	0.1
105	-1.8	0.1	-3.4	0.1
110	0.3	0.1	-1.8	0.1
115	-0.7	0.1	-2.9	0.1
BULK	-1.8	0.1	-3.6	0.1

Table S5. Sequential δ^{13} C and δ^{18} O measurements from fossil Elephantidae (Specimen WNEF17_1/217) analysed in this study.



Figure S3. Sequential δ^{13} C and δ^{18} O measurements from fossil Elephantidae (specimens WNEF17-1 217) analysed in this study.

Appendix C. List of Mio-Plio-Pleistocene hominin footprint sites

Table S6. List of Mio-Plio-Pleistocene hominin footprint sites. Tableexpanded on from Lockley et al. (2008, Table 2).

Site	Age	Approx. date in years BP
Trachilos, Greece (?)	Late Miocene	5,700,000
Laetoli, Tanzania	Pliocene	3,7000,000
Koobi Fora, Kenya	Early Pleistocene	1,500,000
Ileret, Kenya	Early Pleistocene	1,500,000
Happisburg, UK	Early Pleistocene	1,000,000 - 780,000
Gombore II-2, Ethiopia	Middle Pleistocene	700,000
Roccamonfina, Italy	Middle Pleistocene	385,000 - 325,000
Terra Amata, France	Middle Pleistocene	400,000 - 300,000
Nahoon, South Africa	Late Pleistocene	127,000
Alathar, Saudi Arabia	Late Pleistocene	121,000 - 112,000
Langebaan, South Africa	Late Pleistocene	117,000
Cape south coast, South Africa	Late Pleistocene	90,000
Vârtop Cave, Romanis	Late Pleistocene	62,000
Theopetra Cave, Greece	Late Pleistocene	45,000
Valsequillo, Mexico	Late Pleistocene	
Chauvet Cave, France	Late Pleistocene	30,000 - 20,000
Willandra, Australia	Late Pleistocene	23,000 - 19,000
Lascaux, France	Late Pleistocene	
Niaux, France	Late Pleistocene	
Grotte Aldéne, France	Late Pleistocene	15,000 - 8,000
Peche Merle, France	Late Pleistocene	
Fontanot, France	Late Pleistocene	
Ariege, France	Late Pleistocene	
Tana della Basura, Italy	Late Pleistocene	
Willandra, Australia	Late Pleistocene	
Lhasa region, Tibet	Late Pleistocene	20,000
Ojo Guarena, Spain	Late Pleistocene	15,600
Jeju Island, Korea	Late Pleistocene	15,000
Monte Verde, Chile	Late Pleistocene	12,500
Buenos Aires, Argentina	Late Pleistocene	11,500
Lake Bogoria, Kenya	Late Pleistocene	
Engare Sero, Tanzania	Late Pleistocene	

CHAPTER SIX

Fossils in the desert: A taxonomic and taphonomic study of fossil deposits from the western Nefud Desert, Saudi Arabia

Mathew Stewart

ABSTRACT

Over the past decade, a growing interest has developed on the archaeology, palaeontology, and palaeoenvironments of the Arabian Peninsula. It is now clear that Pleistocene hominins repeatedly dispersed into Arabia, notably during the pluvial interglacial periods when much of the peninsula was characterised by a semi-arid grassland environment. During the intervening glacial phases, however, grasslands were replaced with arid and hyper-arid deserts. These millennia-scale climatic fluctuations have subjected fossils to a dramatic suite of environmental and weathering conditions. Yet, as relatively few palaeontological assemblages have been reported from the Pleistocene of Arabia, our understanding of the preservational pathways that skeletal elements can take in these types of environments is lacking. Here, I report a detailed taxonomic and taphonomic assessment of new and old circum-lacustrine fossil deposits from the western Nefud Desert, Saudi Arabia. Fossil fauna are consistent with a well-watered semi-arid grassland environment and I report, for the first time in the Arabian Pleistocene fossil record, remains of Nesokia, cf. Rattus, and *Hippotragus.* Likewise, the taphonomic results suggest that bones were deposited under more humid conditions than present in the region today. However, fossil deposits in Arabia often exhibit significant attrition, obscuring and fragmenting most finds. These are likely tied to wind abrasion, insolation, and salt weathering following fossilisation and exposure, processes particularly prevalent in desert environments.

INTRODUCTION

The presence of palaeolake deposits documenting past pluvial periods within the hyper-arid Arabian sand seas have long been recognised (Philby, 1933; McClure 1978, 1984; Garrard et al., 1981; Schulz and Whitney, 1985, 1986). In recent years, the number of geomorphological studies of lacustrine and palustrine deposits has increased significantly (e.g. Rosenberg et al., 2011, 2013; Groucutt et al., 2015a, 2018; Parton et al., 2015, 2018) and thousands of discrete palaeolakes and other wetland deposits have been identified in the western Nefud Desert alone (Breeze et al., 2015, 2016). Lake and wetland formation were most prevalent during the middle and late Pleistocene (Rosenberg et al., 2011, 2013; Parton et al., 2015, 2018) and generally coincided with peak interglacials (Drake et al., 2013; Parton et al., 2018), during which the northward displacement of the intertropical convergence zone (ITCZ) carried intensified African summer monsoonal rains over Arabia (Fleitmann et al., 2011; Rosenberg et al., 2013; Jennings et al., 2015). This saw the intermittent transformation of the Saharo-Arabian belt into a semi-arid grassland and the concomitant dispersal of East African savanna taxa into North Africa (Drake et al., 2011; Drake and Blench, 2017) and Arabia (Thomas et al., 1998; Stimpson et al., 2015, 2016; Groucutt et al., 2018).

Hominin occupation of Arabia during interglacial periods is now well-documented in the archaeological record (Groucutt and Petraglia, 2012; Groucutt et al., 2018). River and lake margin habitats were clearly important localities in the landscape for hominins, as evidenced by the recovery of a wealth of Palaeolithic material from and around palaeolacustrine and palaeoriverine deposits (Petraglia et al., 2011, 2012; Groucutt et al., 2015a, b; Scerri et al., 2015; Breeze et al., 2017; Shipton et al., 2014, 2018). Indeed, lake and river margins were important and extensively utilised by Pleistocene hominins in similar semi-arid grassland settings in East Africa (Potts et al., 1999; Clark et al., 2003; Basell, 2008; Roach et al., 2016), as they are by modern hunter-gatherer groups today, such as the Hadza (O'Connell, 2002). Considering the clear importance of the Arabian Peninsula in hominin prehistory, and the regular occurrence of spatially associated fossils and lithic artefacts at palaeolake sites within the Arabian interior (e.g. Scerri et al., 2015; Breeze et al., 2017; Groucutt et al., 2018; Roberts et al., 2018; Stewart et al., 2018), it is crucial to develop an understanding of the preservational pathways that skeletal elements in these environments might take.

Fortunately, the need for taphonomic frameworks with which to study large vertebrate fossil assemblages has long been recognised and a wealth of actualistic and naturalistic landscape studies within semi-arid grassland settings have been conducted and applied to questions surrounding early hominin and animal landscape use, interactions, and behaviour (e.g. Behrensmeyer, 1978; Behrensmeyer and Dechant Boaz, 1980; Blumenchine, 1986, 1988, 1989; Domínguez-Rodrigo, 2001; Faith and Behrensmeyer, 2006; Faith et al., 2007). Much of this research has been drawn upon and discussed in previous chapters. Considerably less attention, however, has been devoted to understanding the taphonomic processes operating in desert environments (e.g. Andrews and Whybrow, 2005; Denys et al., 2007). It is important that these are considered when working in Arabia, and other similar areas (e.g. the Sahara), where the climate has alternated between humid and hyper-arid over millennia, potentially exposing bones and fossils to a suite of environmental conditions and preservation pathways. The importance of this is propounded by the rapid sediment deflation and depositional hiatuses that desert environments are prone to (Parton et al., 2018). These processes prolong deposition and facilitate exhumation of fossils (as well as stone tool deposits). Indeed, a wealth of palaeontological and archaeological material has been recorded scattered atop and eroding out of Pleistocene palaeolake

deposits in the western Nefud Desert (Thomas et al., 1998; Scerri et al., 2015; Breeze et al., 2017; Groucutt et al., forthcoming). Once on the surface, fossils are exposed to additional attritional processes that may significantly modify fossil appearance and assemblage composition (Denys et al., 2007). This is likely to be particularly pronounced in desert environments, which are subject to extreme temperature fluctuations, frost, strong winds, sandstorms, and rare but intense downpour events. The Nefud Desert is no exception. Extreme diurnal temperature variations cause rocks to fracture and exfoliate and fragmentary material produced by this process fills the Nefud Desert dune field (Edgell, 2006). Winter temperatures can reach below freezing and snow occasionally falls across northern Arabia, while strong winds between February and June sometimes incite severe sandstorms (Edgell, 2006).

Here I report a detailed taxonomic and taphonomic assessment of Arabian fossil deposits. Fossils were recovered by the Palaeodeserts Project during fieldtrips conducted between 2013–2016 in the western Nefud Desert, north Saudi Arabia, and in almost all cases were found alongside lithic artefacts. Fossils include both surface and excavated (those found within or partially within sediments) findings, and some of the sites discussed here have been reported on previously (see below). While many of the fossils and lithic artefacts are represented by surface finds, they are typically recovered from spatially restricted areas associated with particular deposits with which they can be quite reasonably associated. The aim of this study is to develop an understanding of the common taphonomic processes that dictated fossil assemblage accumulation in Arabian lake settings, and those that continue to modify fossil assemblages today.

Previous investigations

The site of Khall Amayshan-1 (KAM-1 or "Thomas loc-1") has been previously investigated by various researchers (Thomas et al., 1998;

374

Rosenberg et al., 2013; Scerri et al., 2015). The site consists of a palaeolake deposit situated within an interdunal depression and elevated up to 2.5 m above the basin floor (Scerri et al., 2015). The palaeolake sequence comprises interdigitated marls, silts, and sands indicating lake level fluctuations throughout its existence (Rosenberg et al., 2013; Scerri et al., 2015). Diatoms are dominated by freshwater species (e.g. Fragilaria brevistriata, Aulacoseira crenulata) (Rosenberg et al., 2013). The shift from diatomaceous marls to calcareous sands and lake marls moving up the sequence and an increase in the abundance of periphytic diatoms (e.g. A. crenulata) in the upper units indicate a shallowing of the lake through time (Rosenberg et al., 2013). Thomas et al. (1998) recovered fossils from the surface of the palaeolake and initially attributed the site to the early Pleistocene based on an interpretation of a mostly extinct faunal assemblage that included *Pelorovis* sp. cf. P. oldowayensis and tentatively attributed Hexaprotodon (Thomas et al., 1998). However, subsequent investigations of the site using optically stimulated luminescence (OSL) dating found the palaeolake deposit directly beneath the fossils to be 117 ± 8 ka to 99 ± 7 ka (Rosenberg et al., 2013). Rosenberg et al. (2013), in their stratigraphic log of the site (their Figure 12), indicated that fossils were present in the uppermost marl unit (c. 30 cm) and in the underlying calcareous sands (c. 50-60 cm) but provided no details on the remains themselves. Scerri et al. (2015) also noted fossils scattered on the surface of the palaeolake deposit and reported 106 Middle Palaeolithic lithics artefacts. Artefacts were made of both local (quartzite) and non-local (chert) material and the assemblage was interpreted as representing several discrete Middle Palaeolithic flaking episodes indicating repeated use of the lake by late Pleistocene hominins.

A second site just north of KAM-1, dubbed Khall Amayshan-4 (KAM-4), comprises six distinct palaeolake deposits – northwest (NW) lake, northeast (NE) lake, south (S) lake, southwest (SW) lake, southeast (SE) lake, and central lake (Fig. 2). Each palaeolake deposit was associated with a discrete lithic artefact assemblage ranging from Acheulean to Middle Palaeolithic, suggesting that lake formation at the site was not contemporaneous (Scerri et al., 2015). Acheulean artefacts were made mostly from local quartzites, whereas the later Middle Palaeolithic artefacts were made of both local and non-local materials (e.g. rhyolite, chert) and included abundant stone flakes indicating that knapping took place on the site (Scerri et al., 2015).

An additional site located a few kilometres northeast of KAM-4, dubbed 16.3, was also investigated by Rosenberg et al. (2013). The deposit consists of a ~170 cm thick laminated white diatomite underlain by white sands dated by OSL to 99 ± 7 ka. Rosenberg et al. (2011, 2013) found that the aeolian sediments underlying palaeolake deposits typically predated lake formation by only a few thousand years, suggesting lake onset lies close to the OSL date of 99 ka. Diatom analysis demonstrated an abundance of freshwater species and a gradual change toward a dominance of planktonic and facultatively planktonic taxa (e.g. *F. brevistiata* and *Cyclotella ocellata*) indicating a transition to deeper waters moving up the sequence (Rosenberg et al., 2013; Fig. 12b). Burrows, tentatively identified as being from crayfish, are present throughout the sequence.



Figure 1. Map of fossil localities mentioned in the text (inset taken from Breeze et al., [2017]).

METHODS

Surveys

The 2013–2016 surveys focused on palaeohydrological features (i.e. relict lakes and rivers) owing to their importance as palaeoenvironmental proxies and high potential to yield archaeological and palaeontological material, as demonstrated by previous research (e.g. Petraglia et al., 2012; Rosenberg et al., 2013; Scerri et al., 2015; Stimpson et al., 2016). Palaeolakes were identified via remote sensing (see Breeze et al., 2015) and were investigated on both the fringe of the present-day dune field (via four-wheel drive vehicles) and deeper into the desert interior (via helicopter, provided by colleagues from the Saudi Geological Survey) (Fig. 1). A total of 40 sites were investigated, most of which yielded significant environmental archives, many

with lithic artefacts, and some with fossils (see Breeze et al., 2017 for additional details). Ten of the fossil-bearing deposits are reported in the present study. Pedestrian surveys were conducted across each site and such that the entirety of the palaeolake deposits were examined. All fossils, regardless of size, were plotted using a total station or differential global positioning systems (DGPS), given a unique identifier number, and collected. Shallow excavations (using trowels and brushes) were conducted at two other sites (16.3, WNEF16_1) to recover fossils that were found eroding out of the palaeolake surfaces. The discovery of fossils eroding out of the fringe of the KAM-4 NW lake palaeolake prompted the excavation of four 2x2 m trenches (Fig. 2). Excavations focused on the palaeolake sediments, which extended ~120 cm before reaching the underlying sterile dune sands. All sediment was sieved through a 2mm mesh and all fossils were collected.

Taphonomy and taxonomy

Taphonomic analysis was conducted following the methods described in *Chapters Three* and *Four*. Each fossil specimen was identified to the lowest taxonomic level possible facilitated by comparisons with the osteological collections housed at the Australian National University (ANU) and University of New South Wales (UNSW), Australia. Comparative morphological and morphometric data for selected bovids was collected from the Smithsonian Institution National Museum of Natural History (NMNH) (Appendix A, Table S2). All morphometric measurements were taken following von den Driesch (1976) and Walker (1985). Despite the poor preservation of many of the fossil assemblages discussed here, no analytical winnowing was performed to maintain robust sample sizes. It is acknowledged, however, that analytical winnowing is common practice in taphonomic studies, and that comparisons raised in the discussion include assemblages that have undergone this process. Statistical analyses were carried out in custom-written script in RStudio (RStudio Team, 2015) and PAST (Hammer et al., 2001).

RESULTS AND DISCUSSION

Study sites

All sites reported here comprise inverted relief outcrops of ancient lake deposits situated in interdunal depressions within the western Nefud Desert, attesting to the significant sediment erosion and deflation of palaeolake sediments in the region. While direct dates are only available for three of the sites discussed here (KAM-1, KAM-4 NW lake, 16.3) it is likely that the deposits date to the Pleistocene. Indeed, all dated palaeolake sequences in the western Nefud Desert can be tied to the humid periods of the middle and late Pleistocene and, rarely, the Holocene.

At KAM-1, fossils were recovered from and atop the uppermost marl unit (see Rosenberg et al., 2013, and Scerri et al., 2015 for detailed description of the entire sequence). It should be noted that Thomas et al. (1998) also collected fossils at this site which are not included in this analysis, and therefore the fossils studied here may not be an accurate reflection of the original taphocoenosis. That said, the KAM-1 assemblage described here is, in terms of taxa represented, similar to that reported by Thomas et al. (1998). To the best of my knowledge, no other fossils have been collected from the other sites discussed here.

Renewed investigations at KAM-4 revealed additional palaeolake deposits. Fossils were recovered from the surface of the KAM-4 NW, NE, and S palaeolake deposits, and some finds (n=21) were found during excavations of the former. This is the first time *in situ* finds have been reported from the site. Surface fossils at the KAM-4 NW lake were found concentrated on a



sandy area between two of the trenches and is interpreted as an ancient sandpit that led into the lake.

Figure 2. Map of KAM-4 showing the position of the different lakes and lake boundaries, trenches, and fossils (left), and full sedimentary sequence of the fossil bearing deposits (right). Stratigraphic logs were provided by Richard Clark-Wilson.

Renewed investigations at site 16.3 showed additional sandy marl sediments situated above the upper diatomite unit that were not recognised by Rosenberg et al. (2013), perhaps because they were only preserved in some sections of the site (Fig. 3). These consisted of silty sediments capped by a sandstone-like sandy marl and are interpreted as representing the final desiccation phase of the lake, meaning that the sequence records an entire dry-wet-dry cycle. The recovery of fossils from areas where the sandstone was eroding suggests that bones were deposited as the lake was drying. Most fossils were found on the surface of the palaeolake and concentrated in the southern half of the deposit, while at the centre of the palaeolake a single *Pelorovis* skeleton was found eroding out of the surface of the palaeolake sediment.



Figure 3. Map of the 16.3 site showing the location of the fossils and *Pelorovis* skeleton (left) and full stratigraphic log (right). Stratigraphic logs were provided by Richard Clark-Wilson.

Pedestrian surveys were conducted at the remaining palaeolake discussed here (WNEF16_1, WNEF16_20, WNEF16_22, WNEF16_25). Fossils were typically recovered on the flanks of these deposits where sediments had been eroded and recovered in low-densities, except at WNEF16_1 where fossils were found in a dense 1 m² concentration likely representing an individual carcass.

Systematic palaeontology

Order TESTUDINES Batsch, 1788

Material. – 16.3: two plastron fragments (16.3/255 and 256) and a single vertebra (16.3/405); WNEF16_20: three carapace fragments (unnumbered).

Description. – two small turtle plastron fragments between 4 mm and 6 mm in thickness. A single, poorly preserved vertebrae with maximum length and width of 27.7 mm and 21.4 mm, respectively. Given the fragmentary nature of these specimens, little more can be said regarding their taxonomy.

Order **STUTHIONIFORMES** Latham, 1790 Family **STRUTHIONIDAE** Vigors, 1825 Genus *Struthio* Linnaeus, 1758 *Struthio* sp.

Material. – KAM-4 S lake: a single eggshell fragment (unnumbered); KAM-4 NW lake: two eggshell fragments (KAM16/547 and unnumbered).

Description and remarks. – Thick eggshell fragments (Fig. 5C) with a mostly smooth surface and pores tightly concentrated in shallow circular to semi-circular pits are referred to as ostrich eggshell. Shell thickness measured 2.0 mm and pit diameter measured between 0.5–0.75 mm, consistent with late Pleistocene ostrich eggshell recovered from sites in Asia (Shani et al., 1989; Blinkhorn et al., 2015) and Africa (Texier et al., 2013).

Class AVES Linnaeus, 1758

Referred material. – 16.3: coracoid bone (16.3/259); KAM-4 NW lake: a humerus (KAM4/1), proximal femur (unnumbered), distal tarsometatarsus (unnumbered), metapodial (KAM4/294), distal second metacarpal (unnumbered), and two distal phalanges (KAM16/301 and unnumbered).

Remarks. – Various small bird bones were recovered, but all are fragmented and provide no further diagnostic characteristics.

Order **RODENTIA** Bowdich, 1821 Family **MURIDAE** Illiger, 1811 Genus *Rattus* Fischer de Waldheim, 1803 cf. *Rattus* sp.

Material. – KAM-4 NW lake: left mandible with M_2 and M_3 in place (KAM-4/290).

Description and remarks. – Teeth are rooted, low-crowned, heavily worn and exhibit a simple occlusal pattern (Fig. 5B). The M_3 is triangular in outline, whereas the M_2 is square and with two buccolingually arranged lophs. The preserved tooth-row length is 4.9 mm, and the complete tooth row length (M_1 – M_3) is estimated to be 7.3 mm. Most species of Dipodidae and Gerbillinae can be discounted either on their more complex occlusal pattern and/or small size. *Paradipus* is consistent in size and simple occlusal planform, but they typically exhibit infundibulum and lack enamel on the buccal and lingual surfaces of their molars, features which are absent in the KAM-4 specimen. It is clear from the M_1 root cavity that the anterior-most root protruded mesially, similar to that seen in species of Muridae, and the KAM-4 NW lake specimen closely resembles comparative specimens of heavily worn *Rattus rattus* molars and is consistent in size. The KAM-4 specimen is tentatively attributed to *Rattus* sp. accordingly.

Genus **Nesokia** Gray, 1842 Nesokia sp.

Material. – KAM-4 NW lake: left maxilla with M^1 and M^2 in place (KAM-4/002).

Description and remarks. – Left maxilla with large, fully hypsodont molars and strongly developed lophs is clearly that of a *Nesokia* sp. (Fig. 5A). M^1 and M^2 have a combined length of 6 mm. Individual cusps are still visible suggesting the tooth is in early stages of wear.

Order **PROBOSCIDEA** Illiger, 1811 Family **ELEPHANTIDAE** Linnaeus, 1758 Elephantidae sp.

Material. – KAM-4 NW lake: various tooth enamel fragments (KAM16/292, unnumbered).

Description and remarks. – Tooth enamel fragments were recovered and clearly belong to an elephant, but the fragments are small and poorly preserved and little more can be said regarding their taxonomy.

Order **PERRISODACTYLA** Owen, 1848 Family **EQUIDAE** Gray, 1821 Genus *Equus* Linnaeus, 1758 *Equus* sp.

Material. – KAM-4 NW lake: intermediate phalanx (KAM16/272).

Description and remarks. – An intermediate phalanx (KAM16/272) is clearly that of an equid (Fig. 5D). It is far too large to be one of the wild asses and its length is consistent with the large African Equus greyvi, some species of extinct Eurasian stenonoid horses (i.e. E. altidens and E. suessenbornensis), and wild horse (E. ferus ferus) (Appendix A, Table S1). A principal component analysis (PCA) using five metric variables – greatest length (47.7 mm), smallest breadth (38.9 mm), proximal greatest breadth (50.2 mm), proximal greatest depth (31.5 mm), and distal breadth (38.3 mm) – was conducted and found the KAM-4 specimen to be most similar to E. altidens and E. grevyi (Fig. 4). However, given the poor preservation of the specimen, and the fact that the PCA analysis did not discriminate well among taxa on either axis, the KAM-4 specimen is referred to the genus level only.





385

Order **ARTIODACTYLA** Owen, 1848 Family **HIPPOPOTAMIDAE** Gray, 1921 Genus *Hippopotamus* Linnaeus, 1758 *Hippopotamus amphibius* Linnaeus, 1758

Referred material. – KAM-1: right third metacarpal (KAM-1/F34); 16.3: two left (16.3/51, 210) and one right (16.3/437) astragali, four distal metapodials (16.3/33, 84, 111, 385), and proximal, intermediate, and distal phalanges (16.2/82, 334B, 334A).

Description and remarks. - A metacarpal recovered from KAM-1 (KAM-1/F34) is referred to a hippopotamid (Fig. 6B). The specimen is bleached white and exhibits cortical exfoliation probably due to wind erosion. The proximal articular surface is triangular in outline and dips to the palmar, while the lateral side extends substantially further to the proximal than does the medial side, consistent with the third metacarpal of the right forefoot. Its size fits well-within the range of modern *Hippopotamus amphibius* (Table 1) and is far too large to be considered Hex. liberiensis. Thomas et al (1998) also reported numerous hippopotamid remains from KAM-1. Only a single element was described – a fifth metacarpal (JM 301) "morphologically similar to that of *Hippopotamus*" but "much more slender" and tentatively referred it to Hexaprotodon (Thomas et al., 1998; p. 148). The authors were probably somewhat influenced by their early Pleistocene interpretation of the site and belief that *Hexaprotodon* occupied the region up until the Holocene (Thomas et al., 1998). Thomas et al. (1998), however, was incorrect in both these assertions. Recent OSL dating found that the KAM-1 lake deposit dated to the late Pleistocene (Rosenberg et al., 2013), while *Hip. amphibius* is the only known hippopotamid to have occupied Africa and southwest Asia during this time (Stewart et al., 2017). The material described here, and probably the material reported by Thomas et al. (1998), can be referred to *Hip. amphibius*.

	KAM-1/F34	H. amphibius
Length (mm)	129.5	122-155
Proximal diameter (mm)		
- Anteroposterior	46.1	40-51
- Mediolateral	56.3	43-55
Midshaft diameter (mm)		
- Anteroposterior	23.3	20-23
- Mediolateral	39.4	31-40

Table 1. Measurement of the *Hippopotamus* third metacarpal (KAM-1/F34)and comparative data from Hooijer and Singer (1961).

Hippopotamid remains are relatively abundant at 16.3 (n=23) and consist primarily of fragmented appendicular and axial remains. A well-preserved and complete right astragalus (16.3/51) is too large and squamate to be that of a *Hexaprotodon* sp. and is consistent in overall shape and size to Hip. amphibius (Fig. 6A, Table 2). Two additional astragali (16.3/210, 437), preserving only the distal end, are of similar size and morphology (Fig. 6A). Three distal metapodial fragments (16.3/84, 111, 385), representing the 3rd or 4th metapodials, resemble those of *Hip. amphibius* in their large width and horizontally positioned distal epiphyses (Fig. 6D, Table 3), which contrast to the more obliquely placed distal epiphyses of *Hex*. liberiensis (Hooijer, 1950). A smaller and more obliquely positioned distal metapodial (16.3/33) may represents a 2nd or 5th metapodial and, if correct, is too large to be considered Hex. liberiensis (Table 3). Two robust proximal phalanges (16.3/35, 82) can be attributed to either the 2nd or 3rd digits, one of which can be referred to as a juvenile on the basis of its unfused (and absent) proximal epiphysis (Fig. 5C). A distal phalanx (16.3/334A) with a greatest breadth measuring 27 mm, and a poorly preserved intermediate phalanx (16.3/334B), are also referred to *Hippopotamus*. Given the late Pleistocene age of the lake with which the fossil remains are associated (Rosenberg et al., 2013) and similarities between the hippopotamid fossils and *Hip. amphibius*, the 16.3 remains are attributed to the extant *Hip. amphibius* accordingly.

Table 2. Measurements of fossil *Hip. amphibius* astragali (16.3/51, 210, 437) from 16.3 and recent comparative data from Hooijer (1950), Faure (1985), and Weston (2003).

	16.3/ 51	16.3/ 437	16.3/ 210	Hip. amphibius	Hex. liberiensis
Max. length (mm)					
- Lateral	89.9	_	_	77–106 (<i>n</i> =28)	46–55 (<i>n</i> =15)
- Medial	77.8	-	_	_	—
- Median	82.3	_	_	-	—
Max. width (mm)					
- Distal	78.9	77.4	$\sim\!92.5$	59–98 (n=30)	30–40 (<i>n</i> =15)
- Proximal	74.4	_	_	_	_
Breadth/length index	87.8	_	_	76.5–92.3 (<i>n</i> =10)	70.0–73.9 (<i>n</i> =5)

Table 3. Measurements of fossil *Hip. amphibus* metapodials (16.3/33, 84, 111, 385) from 16.3 and recent comparative data from Hooijer (1950), Hooijer and Singer (1961), and Faure (1985). Comparative data has been pooled across the metapodials (i.e. 3rd and 4th metapodial data pooled and 2nd and 5th metapodial pooled).

Element	Measure	16.3/	16.3/	16.3/	16.3/	Hip.	Hex.
		33	84	111	384	amphibius	liberiensis
Distal 3rd/4th	Distal	_	42.0	46.0	46.0	34-48	—
metapodial	width					(<i>n</i> =11)	
	(mm)						
Distal 2 nd /5 th	Distal	33.0	_	_	_	28-46	18
metapodial	width					(<i>n</i> =31)	(<i>n</i> =1)
	(mm)						

Hippopotamus sp.

Material. - KAM-4 NW lake: right astragalus (KAM-4/010).

Description and remarks. – A right astragalus (KAM4/010) recovered from KAM-4 NW lake is similar in overall size and morphology to *Hip*. *amphibius* (Fig. 6E). The specimen is, however, poorly preserved and distorted making a specific assignment difficult, and this specimen is referred to *Hippopotamus* sp. accordingly.

cf. Hippopotamus sp.

Material. – KAM-4 NE lake: femur head (KAM-4/7015), distal fibula (KAM-4/7016).

Description and remarks. – Two specimens recovered from KAM-4 NE lake are probably a hippopotamid but are too incomplete to be confidently attributed: a large globular femur head (Fig. 5F) with a diameter of 77.6 mm and a distal fibula.

Family BOVIDAE Gray, 1821Genus *Pelorovis* Duvernoy, 1851*Pelorovis* sp. cf. *P. antiquus* Duvernoy, 1851

Referred material. – 16.3: right distal phalanx (unnumbered), right and left calcaneum (16.3/291 and 16.3/436), and proximal tibia (SGS1060.25); WNEF16_1: single complete M² or M³ (WNEF16_1); KAM-1: left distal humerus (KAM-1/F38).

Description and remarks. – Numerous fossils represent a large buffalo, and while most of the specimens are fragmented, some are complete enough to provide taxonomic insight. A distal phalanx (16.3/unnumbered; Fig. 5G) with a curved plantar surface and poorly developed processes extensorius and tuberculum flexorium is consistent with *Syncerus* and *Pelorovis*, but not *Bos* (Peters, 1986; Thomas et al., 1998). Its length, however, falls outside the size range reported for *Syncerus* and in this respect it probably more closely resembles the larger *Pelorovis* (Table 4). Indeed, its size closely matches the *Pelorovis* sp. cf. *P. oldowayensis* distal phalanx reported from KAM-1 (Thomas et al., 1998). Two calcanea (16.3/291, 436) are consistent with those of *Bos* and *Pelorovis* in size and in exhibiting a short sustentaculum tali and well-developed processes coracoideus, features which are absent in *Syncerus* (Fig. 5F, Table 4; Gentry, 1967; Peters, 1986). A distal metapodial (16.3/SGS/1060.19, Fig. 5I) is larger than those of *Syncerus* and *Bos* but comparable to late Pleistocene *P. antiquus* remains from Africa, while a proximal tibia (16.3/SGS/1060.25) also exceeds the size ranges reported for the *Syncerus* and *Bos* (Table 4). Therefore the 16.3 large bovid material is referred to *Pelorovis* and the late Pleistocene age of the site makes attribution to *P. antiquus* (following the taxonomic nomenclature of Gentry and Gentry, 1978) most likely.

Table 4. Measurements of fossil *Pelorovis* sp. remains and recent and fossil comparative data from Gentry (1967), Peters (1986), and Peters et al. (1990).

Element	Measure (mm)	16.3	KAM- 1	S. caffer	B. taurus	P. antiquus
Humerus	Dist. ep. breadth (BT)	_	103.5	68–89 (<i>n</i> =16)	61–95 (<i>n</i> =18)	_
Tibia	Prox. Breadth (Pb)	151.0	—	89–120 (<i>n</i> =17)	77–128 (<i>n</i> =17)	_
Calcaneum	Greatest length (GL)	153.3	—	118–155 (<i>n</i> =15)	109–173 (<i>n</i> =15)	119–195 (<i>n</i> =4)
Metapodial	Dist. breadth (Bd) Dist. depth (Dd)	$90.6 \\ 47.6$	_		-	
Metacarpal	Distal breadth (Bd)	_	_	54–80 (<i>n</i> =25)	48–83 (<i>n</i> =38)	_
	Distal depth (Dd)	—	—	30.5–40.5 (<i>n</i> =25)	26.5–49 (<i>n</i> =38)	_
Metatarsal	Distal breadth (Bd)	-	_	49–72 (<i>n</i> =24)	43–76 (<i>n</i> =42)	76–101 (<i>n</i> =3)
	Distal depth (Dd)	_	_	31-41.5 (n=24)	24.5-45 (n=42)	44.5 (<i>n</i> =1)
Dist. phalanx	Length of sole (DLS)	94.6	_	59–81 (<i>n</i> =38)	_	83 (<i>n</i> =1)

A large bovid distal humerus (KAM-1/F38) recovered from KAM-1 is also referred to *Pelorovis* as its size exceeds those of *Syncerus* and *Bos* (Table 4). Thomas et al. (1998) also reported remains of *Pelorovis* from KAM-1 which were provisionally attributed to *P. oldowayensis*. However, as discussed elsewhere (Stewart et al., 2017), more recent dating of the KAM-1 palaeolake to the late Pleistocene is suggestive of the younger species *P. antiquus*. The specimen described here, and probably those reported by Thomas et al. (1998), can be provisionally referred to the late Pleistocene *P. antiquus*.

cf. Pelorovis sp.

Referred material. – WNEF16_1: a single complete M^2 or M^3 (WNEF16_1).

Description and remarks. – A single complete M^2 or M^3 (WNEF16_1; Fig. 5E) differs from *Bubalus* in its less complex occlusal outline, while the infundibulum of the distal loop exhibits a marked internal fold as seen in *Syncerus* and *Pelorovis*, and sometimes in *Bos*, albeit typically less pronounced (Martínez-Navarro et al., 2007). The small and simple basal pillar is consistent with *Pelorovis*, whereas those of other large Bovinae are typically more complex and medially pronounced (Gentry, 1967, Fig. 11). That said, rare examples of *S. caffer* with relatively short basal pillars were encountered when examining comparative material. Its size (occlusal length = 31.6 mm, posterior lobe width = 21.3) is comparable to *S. caffer* and *Pelorovis*. The former is unknown from north of the Sahara, while the latter populated Southwest Asia during the Pleistocene (Stewart et al., 2017) and has been reported from nearby localities in the western Nefud Desert (Thomas et al., 1998). Therefore the WNEF16_1 specimen is provisionally attributed to *Pelorovis*.

Subfamily ANTILOPINAE Gray, 1921

Antilopinae sp.

Material. -16.3: right horn core (16.3/416).

Description and remarks. – A small right horn corn (Fig. 5H) with backwards curvature, slight torsion, and some mediolateral compression with a flattened lateral side is clearly that of a gazelle (Gentry and Gentry, 1978). The transverse and anteroposterior diameter measured 21.9 mm and 28.1 mm, respectively. The size and compression index (77.9 mm) are consistent with various species of gazelle, including *Gazella dorcas* and *Nanger soemmeringii* (Gentry, 1964, Gentry and Gentry, 1978).

Subfamily HIPPOTRAGINAE Brooke, 1876 Genus *Hippotragus* Harris, 1838 *Hippotragus* sp.

Material. – WNEF16_25: horn core (WNEF16_25).

Description. – A single fragmented but well-preserved horn core can be attributed to *Hippotragus* (Fig. 5J). The specimen exhibits strong mediolateral compression, and is without torsion, keels, or ridges. The preserved length along the anterior of the horn core is 370 mm, but its original length may have been substantially longer. Given the fragmentary nature of the specimen, and lack of morphometric data, only a generic assignment is possible.

Genus *Oryx* de Blainville, 1816 *Oryx* sp.

Referred material. – 16.3: horn core (16.3/415); KAM-4 Lake S lake: two horn cores (KAM-4/7059, 7088); KAM-4 NW lake: Occipital bone with two partially preserved horn cores (KAM-4/014); WNEF16_20: horn core (WNEF16_20).

Description and remarks. – Small, straight semi-circular horn cores without torsion attributable to *Oryx* were recovered from numerous sites. The basal horn core dimensions of the KAM-4 NW lake specimen (KAM-4/014) are larger than comparative material of the Arabian endemic *O. leucoryx*, smaller than *O. gazella* and *O. beisa*, and within the range of the desert-adapted *O*. dammah (Table 5). The KAM-4 NW lake specimen differs from the latter in having more widely diverging horn cores, but in this regard is comparable to all other living species. It differs from the fossil specimens from the nearby middle Pleistocene site of Ti's al Ghadah in being less robust and having more divergent horn cores (Thomas et al., 1998; Stimpson et al., 2016). Stimpson et al. (2016) suggested that the large and robust *Oryx* fossils from Ti's al Ghadah might represent a now-extinct large-bodied Pleistocene form of *O. leucoryx*. Given the intermediate size of the specimen described here, it's possible that the KAM-4 NW lake specimen represents a transitional form between the large-bodied middle Pleistocene *Oryx* and the smaller, extant Arabian *O. leucoryx*.

Table 5. Measurements of fossil *Oryx* and recent and fossil comparative data (Ti's al Ghadah fossil data from Stimpson et al., 2016).

Measure	KAM-4	Ti's al	O.	O.	O.	O.
	/014	Ghadah	leucoryx	gazella	beisa	dammah
Transverse diameter (mm)	37.5	Mean = 41.15 (<i>n</i> =?)	31–30 (<i>n</i> =3)	40–55 (<i>n</i> =10)	39–44 (n=3)	30–40 (<i>n</i> =4)
Antero- posterior diameter (mm)	32.4	Mean = 43.0 (n=?)	23–30 (<i>n</i> =3)	41–16 (<i>n</i> =10)	36–43 (<i>n</i> =3)	30–39 (<i>n</i> =4)
Horn core	~40	~20–35	~20-40	~35–45	~30–40	~20–30
divergence (°)		(n=?)	(<i>n</i> =6)	(n=3)	(<i>n</i> =3)	(<i>n</i> =3)



Figure 5. (A) left maxilla (KAM-4/002), Nesokia sp.; (B) left mandible (KAM-4/290), cf. Rattus sp.; (C) eggshell fragment (KAM16/547), Struthio sp.; (D) intermediate phalanx (KAM16/272), Equus sp.; (E) M² or M³
(WNEF16_1), cf. Pelorovis sp.; (F) complete (16.3/291) and broken (16.3/436) calcanei, Pelorovis sp. cf. P. antiquus; (G) right distal phalanx (16.3/unnumbered), Pelorovis sp. cf. P. antiquus; (H) right horn core (16.3/416); Antilopinae sp.; (I) distal metapodial (16.3, 16.3/SGS/1060.25), Oryx sp.; (J) horn core (WNEF16_25), Hippotragus sp.; (K) gypsum crystal fossil recovered from the Ti's al Ghadah basin. Scale bars are 30 mm unless specified.



Figure 6. Hippopotamid remains. (A) right (16.3/51) and left (16.3/437) astragali, *Hippopotamus amphibius*; (B) right third metacarpal (KAM-1/F38), *Hip. amphibius*; (C) juvenile proximal phalanx of the 2nd or 3rd digit (16.3/82), *Hip. amphibius*; (D) distal metapodial fragment (16.3/111), *Hip. amphibius*; (E) astragalus (KAM-4/010), *Hippopotamus* sp.; (F) femur head (KAM-4 NE lake, KAM-4/7015), cf. *Hippopotamus*. Scale bars are 30 mm unless specified.

Table 6. Taxonomic list

	-	-	-		KAM-	KAM-4	KAM-4	KAM-4
Class	Order	Family	Taxon	Common name	1	S lake	NW lake	NE lake
Aves		-					-	
	Struthioniformes	Struthionidae	Struthio sp.	Ostrich		х	х	
			Gen. et sp. indet.	Bird			х	
Mammalia								
	Proboscidea	Elephantidae	Gen. et sp. indet.	Elephant			х	
	Rodentia	Muridae	cf. Rattus sp.	Rat			х	
			Nesokia sp.	Bandicoot Rat			х	
	Artiodactula	Hinnonotamidae	Hippopotamus amphibius	Common	v			
	111 tiouacty ia	mppopotamuae		Hippopotamus	А			
			<i>Hippopotamus</i> sp.	Hippopotamus			х	cf.
		Bovidae	Pelorovis sp. cf. P. antiquus	Pelorovis	х			
			cf. Alcelaphini		x*			
			Oryx sp.	Oryx		х	х	
			Size 3 bovid gen et sp. indet.	Large bovid			х	
			Size 2 bovid gen et sp. indet.	Bovid		х	x	X
	Perrisodactyla	Equidae	Equus sp.	Horse	x*		х	

*Taxa listed in Thomas et al., (1998). Taxa listed in bold from *in situ*.

Table 6. Continued.

Class	Order	Family	Taxon	Common name	16.3	WNEF	WNEF	WNEF	WNEF
						16_1	16_20	16_{22}	16_{25}
Reptilia					-	-	-	-	-
	Testudines			Turtle	х		х		
Aves									
			Gen. et sp. indet.	Bird	х				
Mammalia									
				Common					
	Artiodactyla	Hippopotamidae	Hippopotamus amphibius	Hippopotamus	Х				
		Bovidae	Pelorovis sp. cf. P. antiquus	Pelorovis	Х				
			cf. Pelorovis	Pelorovis		х			
			Antilopinae sp.	Gazelle	х				
			<i>Hippotragus</i> sp.	Grazing antelope					Х
			Oryx sp.	Oryx	х		х		
			Size 3/4 bovid gen. et sp. indet.	Very large bovid	Х				
			Size 3 bovid gen et sp. indet.	Large bovid				х	
			Size 2 bovid gen et sp. indet.	Bovid	Х				

Taphonomic analysis

Various taphonomic considerations and their role in shaping the Arabian Pleistocene fossil assemblages will be discussed below. The very small sites (i.e. KAM-4 NW lakeexcavated, WNEF16_20, WNEF16_22, and WNEF16_25) are excluded from discussions unless otherwise specified. The KAM-4 NW lake assemblage is discussed both in terms of the entire assemblage (surface and excavated material) and excavated material only. Full results of the skeletal part representation and taphonomic analysis are presented in Tables 7 and 8, respectively.

<u>Species representation</u>

The current analysis includes 621 identifiable specimens representing at least 12 animal taxa (Table 6). Overall, the fauna identified here are comparable to other Pleistocene sites in the western Nefud Desert (e.g. Stimpson et al., 2016; Groucutt et al., 2018) and included three previously unrecognised taxa in the Arabian Pleistocene fossil record - Nesokia sp., Rattus sp., and Hippotragus sp. The fauna from sites KAM-1 and 16.3, notably *Hippopotamus* and *Pelorovis*, is consistent with palaeoenvironmental data that demonstrates that at times during marine isotope stage 5 (MIS 5; c. 130-80 ka) the western Nefud Desert was significantly more humid and boasted large lakes and grasslands (e.g. Rosenberg et al., 2013; Jennings et al., 2015; Breeze et al., 2016; Groucutt et al., 2018). The presence of Hippopotamus, Nesokia, and elephant at KAM-4 NW lake, which has been loosely tied to MIS 5 on the basis of its associated Middle Palaeolithic technology (Scerri et al., 2015), suggests a similar environmental scenario. While less can be reliably said about the other sites given the small sample sizes and lack of chronological data, the presence of taxa such as *Hippotragus* sp. (as at WNEF16_25), coupled with the accompanying palaeolake sediments and taphonomic evidence (discussed below), suggests that these assemblages were deposited under conditions more humid than characterise the region today. Below the relative abundance of various taxa is discussion with the caveat that sample sizes are small.

Small vertebrates (reptiles, birds, rodents, and small bovids) are best represented in the KAM-4 NW lake (NISP=26, 11.2% of NISP), and particularly so in the excavated portion of the assemblage (NISP=14, 82.4% of NISP). Scarce tortoise carapace, bird, and small mammal fossils were also recovered from sites 16.3, WNEF16_20, and WNEF16_22. At other sites, small animal remains are absent, and overall small animals are drastically underrepresented in the Arabian fossil record. Even today, the hyper-arid Nefud Desert is host to an array of small rodents, lagomorphs, carnivores, and bovids (Harrison and Bates, 1991), and greater precipitation and grassland availability during interglacials (that is, an increase in primary productivity) would have only increased species richness and abundance (the "energy-richness hypothesis") (Hawkins et al., 2003). The scarcity of small animal remains may reflect a sampling bias against smaller and more difficult to spot fossils during pedestrian surveys. This is, in part, supported by the more abundant and diverse small animal assemblages in the excavated portion of the KAM-4 NW lake assemblage, as well as at the nearby sites of Al Wusta (Groucutt et al., 2018) and Ti's al Ghadah (Stimpson et al., 2016). The scarcity of fossils less than 20 mm in length, coupled with the drastic increase in fossil count above this size bracket, also suggests that small fossils were missed during surveys. Alternatively, this bias might be the result of taphonomic processes that preferentially destroy smaller bones, and other researchers have noted that small animals have a reduced chance of being preserved in the fossil record (Behrensmeyer and Dechant Boaz, 1980; Haynes, 1988).

Medium-sized mammals make up the bulk of the Arabian fossil record, most of which can probably be attributed to bovid. Medium-sized bovids are the most common taxon at KAM-4 S lake (NISP=22, MNI=2), KAM-4 NW lake (NISP=32, MNI=3), and KAM-1 (NISP=7, MNI=1), as well as at Al Wusta (Groucutt et al., 2018). *Oryx* represents the only suitably-sized bovid identified at the former two sites, and it seems likely that all or most of the medium-sized bovid fossils from these sites can be attributed to this genus. *Oryx* was also identified at sites 16.3 (NISP=1, MNI=1) and WNEF16_20 (NISP=1, MNI=1), and was the most abundant taxon at Ti's al Ghadah (*Chapter Four*; Stewart et al., 2018). *Hippotragus*, as represented by a single isolated horncore, was the only other medium-sized bovid identified in this study, while remains of Alcelaphini were previously reported from KAM-1 and Ti's al Ghadah (Thomas et al. 1998).

Pelorovis, Hippopotamus, and elephant are the largest animals in the western Nefud Desert fossil record. Large mammals in living populations are often well-represented in the thanatocoenoses (death assemblage) because of the durability and identifiability of their bones. For example, Behrensmeyer and Dechant Boaz (1980) found that 100% of all animals \geq 100 kg in the Amboseli National Park living population were identified in the landscape bone assemblage. While taphonomic processes may have reduced the number of identifiable large mammal species, it's possible that the three large mammal taxa in the Arabian fossil are a good reflection of the large mammal population of Arabia during Pleistocene pluvial periods. Hippopotamus remains are notably common and have now been identified at four or five sites in the western Nefud Desert, as well as further south (McClure, 1984), and are particularly abundant at site 16.3 (NISP=23, MNI=2). The prevalence of Hippopotamus remains is likely a reflection of the research focus on palaeolake deposits.
Fossil appearance

The appearance of fossils varies considerably between sites. Colour ranges from dark brown/maroon through to bleached white (KAM-1; Fig. 7E). The former is indicative of deposition in oxygenated and biologically active soils and implies more humid conditions than at present, while the latter is characteristic of abrasion by fine wind-blown sand (discussed below; but see also Fernández-Jalvo and Andrews, 2016). Black staining by manganese dioxide was noted in seven of the assemblages (Fig. 7G), which most commonly reflects deposition in water or wet sediments but may also be produced during bacterial growth (Fernández-Jalvo and Andrews, 2016).

Root etching was identified in four assemblages, but overall was rarely observed. In some instances, root etching was very deep and similarities between the root marks and fossil surface suggest that etching occurred prior to fossilisation. In contrast, some root marks in the WNEF16_1 and 16.3 site assemblages are more surficial and differ in colour to the surrounding fossil bone indicating etching occurred more recently and following fossilisation (Fig. 7H; Fernández-Jalvo and Andrews, 2016). The latter is interesting in that it suggests that, for at least two of these assemblages, fossils remained near the surface during subsequent humid phases, probably facilitated by slow sedimentation rates and deflation during more arid intervals.

Significant exposure of cancellous bone was noted in the KAM-1 and KAM-4 NW assemblages and is likely the combined result of weathering and wind erosion. In all sites there are rare instances of crushed/distorted bones (e.g. Fig. 7I), and similar bones were recovered nearby at Al Wusta (Groucutt et al., 2018) and Alathar (*Chapter Five*). Distortion differs from typical breakage in that it modifies the shape of the bone without breaking it and is typically the result of long-term sediment compaction (Lyman, 1994). This could be the result of either significant lake sediment build-up or dune migration over the site. Numerous palaeolake deposit have been identified 401

buried or partially buried beneath the present-day sand dunes, indicating some dune movement within the time frame of interest here (Schulz and Whitney, 1986; Breeze et al., 2017). The varying positions of lakes at KAM-4 also suggest that the dune topography shifted substantially between phases of lake formation (Groucutt et al., forthcoming).

Calcrete encrusts the surface of many bones and was sometimes observed within cancellous bone and marrow cavities. This was particularly prevalent in the KAM-1 assemblage and some of the fossils are completely encrusted such that only small portions of the cortical surfaces were exposed. In areas where calcrete is partially eroded, polish and bleaching were noticeably less severe, suggesting that wind-abrasion is an ongoing process. In the 16.3 site assemblage, sandstone was found cemented to the fossils, consistent with the hypothesis that the fossils originated from the top sandstone unit preserved in some section of the site.

Wind abrasion

Many of the fossils across all sites exhibit significant rounding and polish. Such features may result from trampling (Olsen and Shipman, 1988), chemical digestion (Stiner et al., 2012), wind abrasion (Denys et al., 2007), or water-sediment abrasion (Fernández-Jalvo and Andrews, 2003). Distinguishing between agents of abrasion can be difficult, and it is important to consider the context in which the material was recovered, both past and present. Abrasion by digestion and trampling typically produce localized areas of rounding (Fernández-Jalvo and Andrews, 2003), not typically observed in the Nefud fossils. In this regard, abrasion of the fossils is more comparable to water-sediment and/or wind abrasion, consistent with the lacustrine setting in which the bones were originally deposited, and the desert setting in which the fossils were recovered.

Wind abrasion may be particularly prevalent in desert regions where there is abundant sandy substrate and little in terms of vegetation to protect bones (Fernández-Jalvo and Andrews, 2016). Water-sediment abrasion tends to affect the entire surface of a specimen, whereas wind abrasion may be restricted to a single side (i.e. the exposed side) (Denys et al., 2007). Many of the specimens do exhibit rounding, pitting and polish restricted to one side, while retaining sharp, unabraded edges on the other (Fig. 7D). Pitting, more characteristic of wind abrasion, was common in the KAM-1 and KAM-4 NW assemblages. Abrasion varies between the sites and probably reflects time since exhumation. The position in the landscape relative to the surrounding dunes may also play a role, and dunes may protect fossils from abrasion by acting as a wind barrier, or alternatively funnel winds across sites. The KAM-1 assemblage is the most significantly wind abraded, and some fossils have been reduced to near pebbles (Fig. 6F). Abrasion also increases the bone/fossil surface brightness, with fine wind-blown sand having the greatest affect (Fernández-Jalvo and Andrews, 2003, 216). Again, this is most exaggerated at KAM-1, with fossils ranging in colour from light browns and greys to almost pure white (Fig. 6E).

Lastly, it is possible that wind has spatially redistributed fossils. Borrazzo (2016) monitored the effect of wind on lithic artefacts in a desert environment (Fuego-Patagonia) and on sediments comparable to the palaeolake deposits investigated here. Over the course of 11 days winds of up to 90 km/h were found to significantly redistribute artefacts, including moving artefacts of 50 mm in length and 13 g in weight (Borrazzo, 2016). A significant portion of the Arabian fossil record falls below this size and weight. Therefore, wind transport may have significantly redistributed some of the Arabian fossil assemblages, particularly those that have been exposed for a long time. Such a process could explain the contrast between the densely concentrated *Pelorovis* skeleton and the sparsely concentrated loose surface fossils at site 16.3 (Fig. 3).

Weathering

Ascertaining weathering stage for some of the fossils was difficult due to adhering calcrete and substantial wind erosion. Nonetheless, there are apparent similarities in weathering stages across the sites studied here, and across the Arabian Pleistocene fossil record as a whole. Weathering stages 2 and 3 typically dominate, stages 0, 1 and 4 are present but are typically less frequent, and stage 5 is rarely recorded.

The varied weathering pattern observed at large and taxonomically diverse sites such as KAM-4 NW lake and 16.3 probably reflects attritional bone assemblages in which carcasses were continually added to the landscape. Lakes are attractive features in semi-arid settings and deaths by natural causes (e.g. dehydration, predation) can provide a constant input of bones variably affected by weathering processes through time (e.g. Behrensmeyer, 1978; Haynes, 1988). In contrast, the WNEF16_1 assemblage, which comprises a single *Pelorovis* skeleton (n=213) found in a dense onemeter squared concentration, exhibits the full-spectrum of weathering stages. Importantly, this demonstrates that significant variation in weathering can occur across very small spatial and temporal scales. Indeed, during our surveys I observed a camel carcass that, in a single cranium, was partially fleshed below the surface of the sand but exhibited stage 2 weathering above. Andrews and Whybrow (2005) also observed this, albeit not to the extent reported here, when monitoring a single camel carcass in a desert environment over a 15-year period. In that instance, the variation in weathering appears to have been the result of shifting sands covering and protecting small bones such as ribs and vertebrae, while leaving larger bones exposed.

	KAM-	KAM-4	KAM-4	KAM-4	KAM-4	16.3	16.3	WNEF	WNEF	WNEF
		Slake	NW lake	Nw excavated	NE lake	Site	Pelorovis	10_1	16_20	16_22
NRSP	75	67	588	21	17	480	90	213	4	4
NISP	33	37	225	18	9	126	38	102	3	3
NRSP/NISP	2.3	1.8	2.6	1.2	1.8	3.8	2.4	1.2	-	-
Elements	_	_	_	_	_	—	_	_	_	_
Horn core	_	3	1	_	_	4	_	_	1	_
Crania	_	1	1	1	_	3	_	-	_	-
Mandible	_	1	6	1	_	—	—	—	_	_
Isolated tooth	5	1	1	1	_	—	—	3	_	_
Atlas	_	_	-	-	_	—	—	_	_	_
Axis	_	_	1	-	_	—	—	_	_	_
Cerv. vert.	_	_	4	_	_	1	_	-	_	-
Thor. vert.	1	2	12	-	_	1	3	_	_	_
Lumb. vert.	—	_	-	-	-	—	—	-	_	-
Caud. vert.	—	_	-	-	-	—	—	-	_	-
Ind. vert.	1	2	39	1	_	16	—	_	_	1
Rib	—	1	8	-	-	17	—	6	2	1
Scapula	1	_	6	-	-	5	—	-	_	-
Pelvis	—	_	-	-	-	—	1	-	_	-
Humerus	2	-	9	1	-	10	_	—	-	-
- Complete	-	—	_	-	_	—	_	—	—	—
- Prox. ep.	-	—	_	-	—	4	_	—	—	-
- Pox. ep. + shaft	1	—	_	-	—	—	_	—	—	-
- MSHF	1	-	2	-	-	_	-	-	-	-
- Dist. ep. + shaft	-	-	2	-	1	1	-	_	-	-
- Dist. ep.	-	-	4	-	_	5	_	_	-	-

 Table 7. Skeletal part representation (NISP).

	KAM-	KAM-4	KAM-4	KAM-4	KAM-4	16.3	16.3	WNEF	WNEF	WNEF
	1	S lake	NW lake	NW excavated	NE lake	Site	Pelorovis	16_1	16_20	16_{22}
Elements										
Radius	1	2	5	1	_	1	1	_	_	_
- Complete	_	_	_	_	_	-	—	_	_	_
- Prox. ep.	_	1	_	-	_	1	_	_	-	_
- Pox. ep. + shaft	1	_	1	_	_	_	_	_	_	_
- MSHF	_	—	_	_	_	—	—	_	—	_
- Dist. ep. + shaft	_	—	2	1	_	-	1	_	—	-
- Dist. ep.	_	1	2	_	_	—	—	—	—	_
Ulna	_	_	2	_	_	1	_	_	_	_
Metacarpal	3	_	4	3	_	_	_	_	_	1
- Complete	1	_	1	_	_	—	—	_	_	_
- Prox. ep.	_	—	1	-	_	-	—	_	—	-
- Pox. ep. + shaft	1	_	1	1	_	_	_	_	_	1
- MSHF	_	—	_	-	_	-	—	_	—	-
- Dist. ep. + shaft	1	—	1	1	_	-	—	_	—	-
- Dist. ep.	-	_	—	_	_	—	—	—	_	_
Femur	2	_	8	1	_	4	3	-	_	_
- Complete	-	_	_	_	_	_	_	_	_	_
- Prox. ep.	_	_	_	_	1	1	1	_	_	_
- Pox. ep. + shaft	2	_	4	1	_	1	_	_	_	_
- MSHF	-	-	1	-	_	-	_	-	-	_
- Dist. ep. + shaft	_	_	1	_	_	_	_	_	_	_
- Dist. ep.	_	-	2	_	_	2	2	_	-	-

Table 7. Continued.

	KAM-1	KAM-4 S lake	KAM-4 NW lake	KAM-4 NW excavated	KAM-4 NE lake	16.3 Site	16.3 Pelorovis	WNEF 16_1	WNEF 16_20	WNEF 16_22
Elements										
Tibia	1	1	8	1	_	5	1	_	_	_
- Complete	_	—	—	-	_	_	_	_	_	_
- Prox. ep.	_	_	_	-	_	2	_	-	-	-
- Pox. ep. + shaft	_	1	2	1	_	_	1	_	_	_
- MSHF	_	—	_	_	_	—	_	_	_	_
- Dist. ep. + shaft	_	—	3	-	—	3	_	-	-	-
- Dist. ep.	_	—	3	-	—	—	_	-	-	_
Fibula	_	_	_	_	2	_	_	_	_	_
Metatarsal	_	_	_	_	_	2	_	_	_	_
- Complete	_	_	_	-	_	1	_	-	-	_
- Prox. ep.	_	—	_	_	_	—	_	_	_	_
- Pox. ep. + shaft	_	—	_	_	_	1	_	_	_	_
- MSHF	_	—	_	_	_	—	_	_	_	_
- Dist. ep. + shaft	_	—	—	-	—	_	_	-	-	-
- Dist. ep.	-	—	—	-	—	—	_	-	-	—
Metapodial	1	3	6	1	—	8	3	1	_	_
- Complete	_	_	_	-	_	_	_	-	-	-
- Prox. ep.	_	—	_	_	_	—	_	_	_	_
- Pox. ep. + shaft	_	1	—	-	—	_	_	-	-	-
- MSHF	_	—	3	-	—	_	_	-	-	-
- Dist. ep. + shaft	_	—	1	-	—	2	1	-	-	_
- Dist. ep.	—	2	2	-	—	6	2	1	-	—
Carpal/Tarsal	_	6	21	1	_	17	4	_	_	_
Phalanges	1	11	11	2	_	8	6	1	_	_
Sacrum	_	_	2	_	_	_	-	_	_	_
Long bone shaft	15	3	59	2	5	22	3	91	_	_

Table 7. Continued.

	KAM-1	KAM-4	KAM-4	KAM-4	KAM-4	16.3	16.3	WNEF	WNEF	WNEF
		S lake	NW lake	NW lake	NE	Site	Pelorovis	16_{1}	16_{20}	16_{22}
				excavated	lake					
Weathering (%)										
0	0	5	5	10	0	26	2	3	0	0
1	3	8	17	2	0	32	16	11	0	0
2	2	27	49	1	4	56	20	64	1	0
3	12	10	101	2	6	68	29	82	2	1
4	9	0	17	2	2	16	6	12	0	1
5	3	0	0	0	0	0	0	1	0	0
Indeterminate	50	15	384	4	5	282	26	40	1	2
Tooth-marked bones	1	10	8	0	5	16	21	0	0	0
(%)	(1.4%)	(14.9%)	(1.4%)	(0%)	(29.0%)	(3.3%)	(23.3%)	(0%)	(0%)	(0%)
Circ. Comp.										
Type 1	4	3	43	0	4	14	3	85	_	_
Type 2	2	0	2	0	0	2	0	0	_	_
Type 3	12	1	14	10	3	6	1	0	_	_
Breakage										
Dry	14	6	36	3	2	12	4	12	_	_
Green	4	2	11	0	2	4	4	42	_	_
Both	1	0	3	0	0	2	0	11	_	_
Voorhies Group	-			-	=	-	-	-	-	-
I	4	5	65	_	-	35	_	_	-	_
I & II	2	11	17	_	_	13	_	_	_	_
II	7	6	38	_	_	24	_	_	_	_
II & III	0	0	7	_	_	0	_	_	_	_
III	0	1	1	_	_	7	_	_	_	_
Tooth/Vertebrae	2.5	0.2	0.02	-	-	0	-	-	-	-
Manganese staining	Y	Y	Y	Y	Y	Y	Ν	N	Y	N
Root etching	N	Y	Y	N	N	N	Y	Y	N	N
Adhering sediment	Calcrete	Calcrete	Calcrete	Calcrete	None	Sandstone	Calcrete	None	None	None

 Table 8. Results of the taphonomic analysis.

	KAM-1	KAM-4 S Lake	KAM-4 NW lake	KAM-4 NW lake	KAM-4 NE lake	16.3 Site	16.3 Pelorovis	WNEF 16_1	WNEF 16_20	WNEF 16_22
				excavated						
Specimen										
length (mm)										
<20	0	0	3	31	0	1	2	3	0	0
20 - 29	1	2	26	38	13	10	13	11	75	0
30-39	8	13	29	0	13	19	37	33	0	0
40-49	13	20	20	6	13	23	18	23	0	0
50 - 59	14	22	12	0	27	14	15	13	0	0
60–69	8	13	4	0	13	10	5	10	25	25
70 - 79	15	25	4	0	7	8	3	4	0	25
80-89	11	18	2	0	7	5	0	1	0	0
90–99	7	11	0	0	0	4	5	0	0	0
>100	21	34	1	25	7	5	5	1	0	50
Specimen										
width (mm)										
<20	0	50	27	65	13	7	29	63	75	0
20 - 29	9	34	40	18	47	28	31	29	25	0
30-39	17	10	20	6	13	25	22	8	0	0
40-49	17	3	7	0	13	19	14	0	0	50
50 - 59	26	3	4	6	7	10	5	0	0	25
60-69	17	0	1	6	0	5	0	0	0	25
70 - 79	9	0	0	0	7	4	0	0	0	0
80-89	4	0	0	0	0	2	0	0	0	0
90-99	0	0	0	0	0	1	0	0	0	0
>100	1	0	0	0	0	0	0	0	0	0

Table 9. Distribution of specimen maximum length and width (%NISP).



Figure 7. (A) carnivore-gnawed bovid astragalus (S lake; KAM-4/7081); (B) bovid distal phalanx with carnivore tooth puncture (S lake; KAM-4/7033); (C) wind eroded vertebra centrum with cancellous bone exposed (NW lake; KAM-4); (D) unidentified fragment displaying rounding and slight bleaching on one side (top) and sharp edges on the other (bottom) (NW lake; KAM-16/95); (E) large midshaft heavily wind abraded and bleach on one side (left) and less bleached and displaying weathering stage 4 on the other (right) (KAM1); (F) heavily wind abraded midshaft fragment of large animal (KAM1); (G) Manganese stained fragment (S lake; KAM4/7033); (H) bovid distal humerus exhibiting post-fossilisation root damage (16.3_3); distorted

thoracic vertebrae (NW lake; KAM16/71).

A test for size-biased (specimen length) weathering found a positive correlation for the 16.3 site (Spearman's rho, $r_s = 0.280$, p < 0.001), WNEF16_1 (Spearman's rho, $r_s = 0.311$, p < 0.001), and KAM-4 NW lake surface (Spearman's rho, $r_s = 0.166$, p = 0.018) assemblages, indicating that smaller bones were less weathered at these sites. However, given the lacustrine setting in which these bones were deposited, more rapid burial of smaller elements by some other means, perhaps trampling, may better explain the observed correlation.

Weathering stage can also provide important information regarding duration of exposure. The scarcity of unweathered bones in the assemblages implies that burial was typically slow, or that bones were regularly re-exposed. Assuming an environmental setting akin to modern East African savannas, and very generally speaking, the bones reported here would have been exposed for c. 2–15 years before burial (following Behrensmeyer, 1978, Table 2). It should be noted, however, that weathering rate varies according to environment, and bones deposited in wooded (Tappen, 1994), temperate (Andrews and Armour-Chelu, 1998), and desert (Andrews and Whybrow, 2005) settings have all been found to weather slower than those in semi-arid grassland settings.

In addition to duration of exposure, physiochemical stresses associated with repeated temperature and moisture fluctuations are known to accelerate bone degradation and weathering (Behrensmeyer, 1978; Haynes, 1988; Pokines et al., 2018). Such processes may be magnified in lacustrine and riverine settings and Hutson (2016) suggested that the poor preservation of fossil assemblages within the South African interior is the result of bone deposition within river, lake, and spring margins. There is evidence that lakes in the western Nefud Desert underwent repeated desiccation and reactivation events (*Chapter Five*; Rosenberg et al., 2013) and it's likely that at least some of the assemblages reported here were affected by lake level fluctuations. This would also help to explain the highly fragmented nature of many of the Arabian fossil assemblages.

Fragmentation may also be exacerbated by insolation and salt weathering, processes particularly pronounced in desert environments. The former process involves the differential expansion and contraction of rock constituents brought on by extreme diurnal temperature variations (Gutiérrez, 2005), whereas the latter involves the precipitation and expansion of salt crystals within rock cracks (Cook and Smalley, 1968; Cooke, 1981). Mehlman (1987) suggested that salt weathering may be the most significant factor driving the breakdown of fossil material at Lake Eyasi. Indeed, the western Nefud Desert palaeolakes contain carbonates and sulphates (Groucutt et al., 2018; see also Fig. 5K) and the dissolution and reprecipitation of these fossil salts would facilitate salt weathering. Salt weathering as a destructive process affecting the Arabian fossil material is supported by salt crystals within the WNEF16_25 horn core, which was found fragmented but retaining its shape in the landscape (Fig. 5J). Bauer (1988, p. 45) also noted that animal teeth from caves in northeast Saudi Arabia were "split and crumbling" due to the formation of gypsum crustal within the lamellae bone.

Carnivores and carnivore damage

No carnivore remains were identified in this study and carnivore remains are often scarce in open-air landscape and fossil assemblage (e.g. Alberdi et al., 2001; Martínez-Navarro et al., 2004; Hutson, 2012). Low carnivore numbers reflect low predator to prey ratios, differences in predator and prey landscape use, and taphonomic processes that bias against smaller, more fragile carnivore remains (Behrensmeyer et al., 1979; Behrensmeyer and Dechant Boaz, 1980; Tappen, 1995). Despite the paucity of carnivore remains in the sites reported here, their presence is inferred from tooth-marked bone (Fig. 7A,B) and carnivore fossils have been recovered at the middle Pleistocene site of Ti's al Ghadah (Thomas et al., 1998; Stimpson et al., 2015, 2016). Large tooth pits (> 9mm in diameter), tooth-notches, and green-fractured bones attests to the presence of large bone crushing carnivores, probably hyena, while small tooth pits (< 2mm in diameter) imply the presence of smaller carnivores. That said, tooth-marked specimens are typically very rare and/or assemblages too small to provide more detailed insights into the role of carnivores as bone accumulators.

The individual *Pelorovis* skeleton from site 16.3 is one possible exception and carnivore tooth marks were identified on 21 specimens: vertebrae (2); ribs (3); distal radius (1); distal femur (1); proximal tibia (1); distal metapodials (3); proximal phalanx (1); sesamoid (1); and bone fragments (8). The frequency of tooth-marked midshafts (36.4%) falls between those for experimental scenarios modelling carnivore-only (i.e. hyena) and hominin-carnivore tooth mark frequencies (Blumenschine, 1995; Capaldo, 1997, 1998; Domínguez-Rodrigo et al., 2007b). The lack of butchery marks and gnawed ribs, epiphyses, and midshaft fragments suggest that carnivores had primary access to the carcass, but whether this represents a predation event or scavenging is difficult to discern.

Similarly low levels of carnivore damage have been noted at other nearby sites in the western Nefud Desert (*Chapter Four*; Stimpson et al., 2016; Groucutt et al., 2018; Stewart et al., 2018). Taphonomic processes (e.g. weathering and wind abrasion) may alter bones such that many of the original bone surface modifications are no longer identifiable in the taphocoenosis (Hutson, 2016). This is certainly the case for many of the bones in this study and it's likely that the role of carnivores in the accumulation of bones within the western Nefud Desert was greater than the current data suggests.

<u>Skeletal part representation</u>

Patterns of skeletal part survivorship can provide meaningful insights into the biotic and abiotic process influencing the accumulation and preservation of bones. This may be particularly insightful here given that poor preservation has destroyed many of the original bone surface modifications useful for making inferences regarding accumulating agents. Overall, skeletal part representation is poor, and unidentifiable fragments dominate across all assemblages (making up two thirds of all material analysed here), followed by midshaft fragments, and small compact bones (carpals, tarsals, phalanges). Abundant dense midshaft fragments and small compact bones suggests many of the assemblages have undergone significant density-mediated attrition. For example, the single Pelorovis skeleton at site WNEF16_1, which comprises cranial, axial, and appendicular elements in a dense concentration, consists mostly of dense midshaft fragments (42% of NRSP, 89% of NISP). The scarcity of dense dental remains is at odds with this, but Behrensmeyer (1978) noted teeth in the Amboseli National Park, Kenya, rapidly disintegrated as a result of surface desiccation. Such a process may explain the scarcity of dental remains in the Nefud fossil assemblages and is perhaps best exemplified at WNEF16_1, where, except for a single complete molar, dental remains are represented by heavily fragmented and fragile enamel and dentine splinters.

The KAM-4 NW lake and 16.3 site assemblages appear to have been less influenced by density-mediate attrition, as suggested by abundant ribs and vertebrae. This is also borne out when testing for a correlation between KAM-4 NW lake medium-sized bovid long bone MNE (Table 10) and bone mineral density; no correlation was found between medium-sized bovid MNE and goat (Spearman's rho, $r_s = -0.079$, p = 0.715) or wildebeest (Spearman's rho, $r_s = -0.192$, p = 0.369) bone mineral density. However, it's likely that this is an artefact of the heavily fragmented long bone portion of this assemblage which can result in an inaccurate under-representation of dense skeletal elements (Clark, 2019; see also Marean et al., 2004). Overall, the results suggest that while density-mediated attrition was significant, it may not fully explain the skeletal part representation across all sites.

Table 10. KAM-4 NW lake medium-sized bovid minimum number of elements (MNE) for selected limb bones

Element	Humerus	Radius	Femur	Tibia	Metacarp.	Metatar.
Portion	Prox. Shaft Dist.	Prox. Shaft Dist.	Prox. Shaft Dist.	Prox. Shaft Dist.	Prox. Shaft Dist.	Prox. Shaft Dist.
MNE	0 3 6	$1 \ 2 \ 3$	$3 \ 3 \ 3$	1 4 6	1 0 0	0 0 0

<u>Water transport</u>

Bones of different densities (and shapes) have different transport potentials in hydrological systems (Voorhies, 1969; Behrensmeyer, 1975; Dechant Boaz and Behrensmeyer, 1976; Fernández-Jalvo and Andrews, 2003) and as a result, assemblages influenced by hydraulic winnowing can be either over or underrepresented in dense skeletal parts. Considering the lacustrine setting in which all these assemblages were situated, it is worth investigating the possibility of such a process. Indeed, previous studies at KAM-1 suggest that the lake underwent frequent lake level fluctuations (Rosenberg et al., 2013) and preliminary analysis of the KAM-4 NW lake sediments found abundant allogenic quartz, low CaCO₃, and "rip up" marls indicative of a high energy lake system (Richard Clark-Wilson pers. comm.).

There is a clear bias towards easily transported elements (i.e. Voorhies Group I and II) in some of the assemblages (Table 3). Importantly, this suggests that these assemblages, or part thereof, may be allochthonous. Hydraulic winnowing is also supported by tooth to vertebrae ratios, which fall outside the range for minimal hydraulic sorting (0.44–1.5). However, low numbers of teeth may also be explained by preferential destruction of dental remains in lacustrine settings and the values reported here are similar to those from non-transported bones from lake margin habitats in the Amboseli National Park (Behrensmeyer and Dechant Boaz, 1980). Only the KAM-1 assemblage falls between the range for minimal and strong hydraulic sorting (3.12–3.48), and considering the large fauna and fossils represented at the site, the assemblage could be interpreted as a lag deposit; although, it is important to remember that Thomas et al. (1998) also collected fossils from the site not included in this analysis. No evidence for water-sediment abrasion could be confidently identified in any of the assemblages, although it is possible that this has been obscured by extensive wind abrasion. While changes in local landscape hydrology are likely to have altered bone accumulations, its specific influence is not currently discernible.

Bone breakage

Bone breakage is ubiquitous, and most long bones are represented by Type 1 specimens (i.e. long bones retaining less than half their original circumference; Bunn, 1982). The KAM-1 assemblage is unique in having more Type 3 bones, which probably reflects the more resilient long bones of the larger animals preserved at the site (*Hippopotamus, Pelorovis*). Hominins and carnivores break open long bones to exploit marrow and as a result generate bone assemblages dominated by Type 1 long bones (Blumenschine, 1986, 1988; Marean and Spencer, 1991; Marean et al., 1992). In all but one case the assemblages were found to statistically differ from the three experimental models simulating carnivore and hominin feeding behaviour (Table 11) (Marean and Spencer, 1991; Marean et al., 1992). Only the 16.3 and KAM-4 NW lake assemblages were indistinguishable from the hammerstone only model. However, as no evidence for butchery was identified, despite the recovery of lithics alongside fossils, a role of hominins in the accumulations of these deposits, or any of the deposits analysed here, is currently not supported. Overall, the results suggest a greater abundance of more complete long bones than assemblages generated experimentally by carnivores or hominins. The findings here probably strongly reflect accumulation in natural settings in which many bones may go undisturbed by large carnivores.

Table 11. Chi-squared test results of long bone shaft circumference completeness compared to those generated during experimental scenarios modelling carnivore (i.e. hyena) and hominin feeding (data from Marean et al., 2004)

	KAM-4 NW lake	16.3	WNEF16_1	KAM-1
Hammerstone only	$\chi^2 = 7.894$	$\chi^2 = 2.270$	$\chi^2 = 35.682$	$\chi^2 = 36.544$
	p = 0.019	p = 0.321	p < 0.001	p < 0.001
Carnivore only	$\chi^2 = 28.066$	$\chi^2 = 23.436$	$\chi^2 = 11.761$	$\chi^2 = 80.335$
	p < 0.001	p < 0.001	p = 0.003	p < 0.001
Hammerstone-	$\chi^2 = 25.492$	$\chi^2 = 20.916$	$\chi^2 = 13.035$	$\chi^2 = 76.430$
Carnivore	p < 0.001	p < 0.001	p = 0.001	p < 0.001

Dry-broken bones dominate almost all assemblages and are likely the result of trampling and post-depositional destruction. Such process would explain the abundance of Type 1 long bones in the absence of evidence for carnivore processing and butchery, although, as emphasized above, it's possible that the role of carnivores, and maybe even that of hominins, has been overshadowed by significant weathering and cortical exfoliation. Green-fractured bones were typically observed in only small numbers, and in many cases can be attributed to carnivore gnawing. Only in the WNEF16_1 assemblage is green-fractured bones more common.

CONCLUSIONS

The fauna identified in this study are broadly similar to those from other sites in the western Nefud Desert (Thomas et al., 1998; Stimpson et al., 2015, 2016; Groucutt et al., 2018) and elsewhere in Arabia (McClure, 1984; Delagnes et al., 2012). In addition, the present study recognises, for the first time in the Arabian Pleistocene fossil record, remains of *Nesokia*, cf. *Rattus*, and *Hippotragus*. The presence of *Hippopotamus*, *Pelorovis*, and *Equus* at sites 16.3 and KAM-1 strongly support the idea that at times during MIS 5 the western Nefud Desert boasted large grasslands and permanent river and lake systems. While the presence of, *Hippopotamus*, *Nesokia*, and elephant at the KAM-4 NW lake suggest similar well-watered conditions. The scarcity of small animals in the deposits studied here is likely the result of sampling bias, taphonomic processes that preferentially destroy small animal remains, or some combination of these.

Similarities in fossil appearance and composition suggests that the Arabian fossil fauna assemblages are the product of shared or similar accumulating and attritional processes. Evidence for root etching, red and black (manganese) staining, and occasional stage 4 and 5 weathering suggest that bones were deposited in settings more humid than characterises the western Nefud Desert today. This is consistent with the lacustrine sediments with which the assemblages are associated, as well as the fauna identified at these sites. The physiochemical stresses associated with lacustrine environments, principally repeated wetting and drying events, likely degraded bone and promoted fragmentation. Physical stress associated with sediment weight, via lake sediment build up or dune migration, furthered fragmentation. The role of carnivores in the accumulation and modification of the Arabian fossil deposits remains difficult to assess, but it seems likely that they played a greater role than the current observations suggest. Perhaps even more significant in the assemblages studied here are the post-exhumation attritional processes, namely those associated with harsh desert environments. Wind abrasion is particularly pronounced in sandy deserts and has significantly modified the assemblages studied here, causing substantial rounding, cortical exfoliation, and bleaching of fossils. This is especially pronounced in the KAM-1 and KAM-4 assemblages, and fossils are strikingly similar in appearance to fossils recovered from the Sahara (see Fernández-Jalvo and Andrews, 2006, Figs. A.565, A.566 and A.578). Salt weathering as a destructive process affecting the Arabian fossil material is supported by the presence of salt crystals in at least one of the fossils analysed here, and similar evidence from cave deposits elsewhere in Arabia (Bauer, 1988). The heavily fragmented geological material that fills the Nefud Desert is thought to be the result of severe insolation weathering (Edgell, 2006), and it seems likely that this process also facilitated the fracturing of fossils over the millennia.

The most notable inter-assemblage differences are between surface and excavated deposits; although, the number of excavated sites is still rather limited and sample sizes small. Those discovered eroding out of palaeolake sediments were found in dense concentrations; the WNEF16_1 assemblage (n=213) was recovered from an area of 1 m², while the *Pelorovis* skeleton at site 16.3 (n=90) was recovered from an area of 3 m². In contrast, loose surface fossils were more sparsely scattered across the palaeolake deposits, which may be the result of wind action, water transport, or animal trampling. Most other inter-assemblage differences (e.g. differences in carnivore gnawing, root etching, etc.) can probably be tied to poor preservation and wind abrasion, which almost certainly reflects time since exhumation. Considering that wind abrasion is most severe at KAM-1, the abundance of large fossils and more complete long bones at this site appears to reflect a true difference in large mammal abundance and long bone completeness. While more work is needed to investigate the impact of desertic processes on fossils, the fossils examined here clearly demonstrate that these processes are highly destructive and have drastically altered fossil appearance and assemblage composition.

A final important observation was the lack of evidence of butchery at any of the sites. For example, at the site WNEF16_1, which is comparatively well-preserved, the lack of butchery marks despite the discovery of fossils in tight association with lithic artefacts demonstrates that there may not be an immediate temporal association between spatially associated objects. This is an important consideration, especially when investigating in arid environments (e.g. the Sahara and Arabia) where rapid sediment deflation and depositional hiatuses promote the mixing of temporally discrete deposits. The results of this study, alongside the very few other studies undertaken in similar settings (Andrews and Whybrow, 2005; Denys et al., 2007), represents a step in the right direction for developing an understanding of the role that deserts play in modifying fossil assemblages.

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APPENDIX

Appendix A: Comparative morphometric data

Table S1. KAM-4 NW lake equid intermediate phalanx (KAM16/272) and comparative data from <u>http://www.vera-eisenmann.com/</u> and Alberdi and Palombo (2013).

	Greatest length	Smallest breadth	Prox. greatest	Prox. greatest	Dist. breadth
	0		breadth	depth	
KAM16/272	47.7	38.9	50.2	31.5	38.3
E. burchelli $(n=46)$	38.7-46.0	31.0 - 39.5	36.5 - 50.2	25.7 - 30.2	33.3-41.2
(n=40) E. f. ferus $(n=2)$	43.0 - 50.5	40.5 - 42.7	50.0 - 53.0	30.5-32.0	44.5-47.5
(n=3) E. f. prezwalskii	41.0-47.0	37.0-43.0	47.0–52.0	27.0 - 35.0	40.0-46.2
(n-1) <i>E. africanus</i> (n=14)	32.0-42.5	30.0-35.0	33.0-42.5	22.0-27.5	29.0-36.0
E. quagga (n=7)	40.0-44.2	34.0-37.0	42.3-46.5	27.0–29.2	36.2-38.0
E. hemionus (n=52)	35.5-45.0	27.8-35.5	32.0-42.0	24.0-28.0	28.9–37.0
E. grevyi (n=28)	43.0–50.0	36.0-42.0	45.0 - 50.5	28.5-33.4	37.0-43.0
$\begin{array}{c} (n & 26) \\ E. zebra \\ (n = 26) \end{array}$	40.0-47.0	34.0-40.0	40.7 - 47.7	27.0-31.0	35.0-39.5
(n-20) E. altidens	42.3–52.7	35.6-42.6	40.9–52.0	27.5 - 36.7	37.0-46.0
(n=10) E. sussenbornensis (n=4)	46.6–50.5	41.8-45.7	49.2–53.4	31.5–36.0	44.4-47.0

Table S2. List of specimens used for comparative data (all data collectedfrom the Smithsonian Institution National Museum of Natural History[NMNH]).

ID	Species
588340	Oryx leucoryx
588247	O. leucoryx
449934	O. dammah
339929	O. dammah
546834	O. dammah
3588333	O. dammah
175786	O. beisa
34687	O. beisa
368528	O. gazella
182128	O. gazella annectens
182129	O. gazella annectens
182193	O. gazella annectens
163216	O. gazella annectens
163218	O. gazella annectens
296154	O. gazella
429190	O. gazella
452648	O. gazella
540012	O. beisa
241366	O. gazella
580535	O. leucoryx
220133	Syncerus caffer
220134	S. caffer
161945	S. caffer
199094	S. caffer
CHAPTER SEVEN

Summary and general conclusions

Mathew Stewart

Summary and conclusions

During the Plio-Pleistocene, orbitally forced increases in environmental variability, aridity, and open grassland habitats resulted in the significant restructuring of African large mammal communities (Vrba, 1985, 1992, 1993; Potts, 1998; Bobe and Behrensmeyer, 2004; deMenocal, 2004). These drastic climatic changes are also considered to have been the driving force behind the speciation and adaptations observed among early Homo and non-Homo homining such as Australopithecus, Ardipithecus, and Paranthropus (Potts, 1998, 2013; Antón et al., 2018). Behavioural and morphological traits include the development of larger brains and bodies, more advanced and persistent toolmaking, increased carnivory, and more complex social cooperation (Antón et al., 2018). Importantly, however, these traits did not arrive as a complete set, say, with the appearance of Homo, but developed over a long period through the evolution of the hominin clade (Antón et al., 2018). Which hominins displayed which traits and how these might be used to distinguish between hominins species remains an intriguing yet challenging area of inquiry. Likewise, the specific role that these intrinsic traits played in the earliest dispersals beyond Africa, of both H. sapiens and earlier Homo species, remains blurred (e.g. Belmaker, 2010; Martínez-Navarro, 2010; Mellars et al., 2013, Groucutt et al., 2015). Notwithstanding its geographical positioning at the nexus of Africa and Eurasia, the Arabian Peninsula has been traditionally excluded from models of hominin and faunal intercontinental dispersals and evolution. This thesis joins a growing corpus of research that is providing a platform with which to consider Arabia into these discussions.

In this thesis I examined the Pleistocene fossil record from the western Nefud Desert, Saudi Araba, which, compared to the archaeological and palaeoenvironmental record, had received little attention (e.g. Thomas et al., 1998; Stimpson et al., 2016, Groucutt et al., 2018). Before sinking my teeth into the fossils themselves, it was first important to consider the mammalian fossil record in a broader temporal and geographical context. In *Chapter Two*, I conducted an extensive review of the large mammal fossil record from Arabia and the surrounding regions, focusing on the last 1 million years. This review revealed various interesting trends and turnover events, as well as potential turnover pulses (i.e. discrete periods of rapid extinction and emergence of new species), in the African and Eurasian mammal palaeocommunities.

Overall, Afro-Eurasian faunal exchange during this period was minimal. One notable exception is the dispersal of various large African carnivore species into Eurasia at around 1 Ma (see also Azzaroli et al., 1988). These faunae are, however, ecological generalist, and their out of Africa dispersal does not necessarily indicate significant environmental change. Indeed, very few herbivore species left Africa around this time, and the origin of some of these taxa has been questioned on taxonomic and biogeographic grounds - that is, some of these taxa have been identified as "Eurasian" species or are thought to have dispersed from Africa much earlier than this time (e.g. Belmaker, 2010). The most notable change in large mammal palaeocommunities occurred in Africa between c.~600-400 ka. This turnover event saw the replacement of many arid grassland-adapted suids, bovids, hippos, and elephants with closely related generalists. As suggested elsewhere (Potts, 1998; Faith, 2014), this evolutionary trend coincided with and was likely driven by heightened environmental variability brought on by the transition to low-frequency high-amplitude glacial-interglacial cycles at around the middle Pleistocene transition (c. 780 ka). Potts (1998) first proposed the "variability selection hypothesis" to explain selection in favour of more versatile taxa in East Africa during the Plio-Pleistocene and extended it as a driving force behind the evolution of *Homo* and its unique traits. The findings presented in Chapter Two fit well-within this framework. Conversely, the large mammal communities of the Levant were far more stable than in contemporary Africa, and extant fauna dominate the Levantine fossil record early on. The lack of intercontinental faunal exchange in the face of significant climate remodelling attests to the ecological separation of these two continents at that time.

Summary and conclusions

This continued into the late Pleistocene and again very few taxa migrated between the continents. In Africa, selection in favour of generalist species may have been even more pronounced during the late Pleistocene (Faith, 2014). Few extinctions occurred in the Levant, and the large mammal community of South Asia was essential 'modern' by *c*. 200 ka (Roberts et al., 2014). In summary, climate change and large mammal community remodelling was far more pronounced in Africa than in southwest and South Asia, there appears to have been no major intercontinental 'migratory waves', nor the extension of African biomes into Eurasia, or *vice versa*. There was, however, some faunal exchange, and this extended into the Arabian Peninsula. Given the presence of various open grassland adapted taxa in the Arabian fossil record, we proposed that hominin dispersals into Arabia would have require no major physiological, cultural, or technological innovations.

The poor Arabian fossil record has made it difficult to draw accurate palaeoenvironmental and palaeoecological inferences, which, in turn, has made testing hypothesis regarding hominin dispersals into the region problematic. Providing detailed insights into the immediate ecology of hominin dispersals into this region was the aim of the study presented in Chapter Three. This study was first inspired by the discovery of lithic artefacts and probably butchered bones at the middle Pleistocene site of Ti's al Ghadah. Significantly, these findings represented the earliest dated evidence for homining in the Arabian Peninsula (c. 500–300 ka). But equally important, this unambiguous hominin presence in association with a large and well-preserved fossil fauna assemblage provided a unique opportunity to investigate past ecological conditions associated with hominin dispersals into and occupation of the Arabian interior. To do so, my colleagues and I conducted stable carbon (δ^{13} C) and oxygen (δ^{18} O) isotope analysis of fossil herbivore teeth found associated with this hominin presence. δ^{13} C values indicated that herbivore diets were dominated by C₄ grasses typical of dry open savannas, consistent with earlier studies (Thomas et al., 1998) and the presence of graze-adapted herbivores (e.g. Palaeoloxodon, alcelaphines). But more insightful, by comparing the δ^{18} O values of obligate and non-obligate drinkers – a useful method for inferring regional aridity, but one rarely employed outside of Africa – we demonstrated that the middle Pleistocene humid periods in the western Nefud Desert were characterised by humidity and precipitation levels akin to those of modern-day East African savannas. Given the savanna-like signal in the Arabian interior, we argued that middle Pleistocene hominin dispersals into this region would have required no major novel adaptation, consistent with hypothesis put forth in *Chapter Two*.

During the arid glacial phases, however, the Arabian interior would have reverted to a hyper-arid desert akin to the conditions that characterise the region today. These millennial-scale humid-arid fluctuations would have exposed bones and fossils to a unique suite of environmental conditions and preservational pathways. However, frameworks with which to study fossil assemblages accumulated under such settings have been lacking, and very few studies have been devoted to understanding the role that desertic processes play in the accumulation and modification of bone and fossil deposits (e.g. Galloway et al., 1989; Andrews and Whybrow, 2005; Denys et al., 2007). Elucidating how dramatic fluctuations in environmental conditions has affected the Arabian fossil deposits was the purpose of the studies presented in Chapter Four and Six. Taphonomic analysis of the fossil assemblages demonstrated that bones were deposited under more humid conditions than present in the region today, consistent with palaeoenvironmental data. However, compared to fossil assemblages from savanna settings, the Arabian fossil deposits exhibit significant attrition, obscuring and fragmenting most finds. This is likely tied to wind abrasion, insolation, and salt weathering following fossilisation and exposure, processes particularly prevalent in desert environments. One key insight from *Chapter Six*, and an important consideration when working in Arabia and other similarly arid environments (e.g. the Sahara), was that sediment deflation and depositional hiatuses may result in the mixing of temporally discrete fossil and stone tool deposits. Taken together, these processes are highly destructive and significantly modify fossil appearance and assemblage composition.

One of the main aims of this thesis was to investigate the interplay between hominins, fauna, and the environment. As discussed in earlier chapters, the types of bones and modifications imparted on their surfaces can provide important clues as to the accumulating and modifying agent/s of fossil assemblages. This has, however, been made rather difficult by the abovementioned destructive processes. Nonetheless, the exceptionally well-preserved Ti's al Ghadah Unit 5 fossil assemblage did provide some interesting insights, the results of which are presented in *Chapters Three* and Four. It's clear that both carnivores and hominins were utilizing the lakeshore for, at the very least, carcass processing. More specifically, the taphonomic study suggests that the assemblage was primarily accumulated by large ambush predators, such as lions and hominins, and subsequently scavenged more durophagus carnivores like hyenas and wolves. Despite the presence of lithic artefacts and probably butchered bone, the anthropogenic signal at the site in rather weak. Given the open lakeside setting and presence of large and potentially dangerous carnivores (e.g. Panthera, Crocuta), it seems possible that hominins were undertaking activities (e.g. carcass processing, lithic artefact preparation) away from the Ti's al Ghadah lake – as has been observed in modern hunter-gatherer groups and inferred for prehistoric hominins (see O'Connell et al., 2002 and references therein). This study provided the first detailed insights into the interplay between hominins, animals, and their environments, and suggests that watering holes have been a focus on the Arabian landscape for resources since the middle Pleistocene.

Finally, the fossil tracks and trackways described in *Chapter Five* provided a unique snapshot into past hominin, fauna, and habitat interactions. Analysis of the palaeolake sediments indicated that the lake was fresh throughout its existence. Importantly, tracks were situated within the palaeolake sequence, as opposed to above it, indicating the presence of hominins and other large mammals in the Arabian interior during a humid phase. Large freshwater lakes would have provided a vital resource and habitable landscape for hominins and fauna alike. Analysis of the tracks and

trackways suggested that hominins and large mammals were occupying the same space and utilising the same freshwater resources across short time scales. I concluded this chapter by arguing, based on the age of the tracks (c. 121–112 ka) and contemporary hominin biogeography, that H. sapiens is likely responsible for the Alathar tracks. Interestingly, this date is contemporaneous with the earliest unambiguous documented evidence for H. sapiens outside of Africa – i.e., the Skhul and Qafzeh early H. sapiens (Grün et al., 2005). This suggests that the earliest dispersals beyond Africa extended into the Arabia interior. Taken together, the studies in this thesis have contributed important new insights into the role of Arabia in hominin prehistory and have shed light on some of palaeoanthropology's outstanding questions.

Where to from here?

Over the past two decades, research in the Arabian Peninsula has produced a great number of exciting new discoveries that has thrown Arabia into the palaeoanthropological spotlight. But still our understanding of the role that Arabia played in hominin prehistory is in its infancy and there remain many gaps in our knowledge that are waiting to be filled. Much of this will depend on continued on-the-ground exploration, and more data from the field will be crucial for testing the hypothesis put forth in this thesis. However, more distant approaches should also be encouraged, the value of which has been highlighted by recent climate modelling (Jennings et al., 2015) and remote sensing (Breeze et al., 2016) studies. As we refine our understanding of past environmental conditions, exploring other avenues such as agent-based models (ABM) of dispersal may help us better understand how hominins may have navigated the landscape; and what's more, such models could help us make better informed decisions regarding which regions to focus our efforts.

Future research should also aim to stray away from the traditional focus on palaeolake deposits and look to new areas in the peninsula. This

Summary and conclusions

research agenda has inherently introduced various geographical, preservational, environmental, and chronological biases into our current dataset. Caves represent a promising avenue for addressing these biases and lacunae. Indeed, there are many large karst and lava tube systems across Arabia and preliminary investigations have identified bones and stone tools within many of these. The next step is obvious!

We should also look to experimental and actualistic studies, drawing inspiration from the decades of work already done in East Africa, to develop a greater understanding of the role deserts play in accumulation and modification bone, fossil, and stone tool deposits. And we should also look outwards. The methods used in *Chapter Three* could and should be applied to other parts of Asia (e.g. the Thar Desert) to investigate how hominins adapted to arid and semi-arid environments as they migrated out of Africa and across the globe.

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APPENDIX

Appendix A. A list of publications that developed during my doctoral studies (see below)

Groucutt, H.S., Grün, R., Zalmout, I.A.S., Drake, N.A., Armitage, S.J., Candy, I., Clark-Wilson, R., Louys, J., Breeze, P.S., Duval, M., Buck, L.T., Kivell, T.L., Pomeroy, E., Stephens, N.B., Stock, J.T., **Stewart, M**., Price, G.J., Kinsley, L., Sung, W.W., Alsharekh, A., Al-Omari, A., Zahir, M., Memesh, A.M., Abdulshakoor, A.J., Al-Masari, A.M., Bahameem, A.A., Al Murayyi, K.M.S., Zahrani, B., Scerri, E.L.M., Petraglia, M.D., 2018. *Homo sapiens* in Arabia by 85,000 years ago. *Nature Ecology & Evolution* 2, 1–10.

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Roberts, P., Stewart, M., Alagaili, A. N., Breeze, P., Candy, I., Drake, N.A.,
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Y.S.A., Zech, J., Alsharekh, A.M., al Omari, A., Boivin, N., Petraglia, M.D.,
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