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

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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 km^2, 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 retreat/extirpation.

Keywords: Pleistocene, Vertebrates, Turnover, Palaeoenvironment, Biogeography

1. Introduction

Major shifts in biogeography and faunal turnovers during the Pleistocene 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 retreats, extirpations/extinctions 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 moderately heavy summer monsoon and persistent light to medium rainfall throughout the year, permitting expansive grasslands; an interpretation supported by the fauna recovered (e.g. *Bos, 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 lake formation, and associated humid periods, occurred ca. 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 (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 such 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 and 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 ^{13}C 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 the Western Nefud 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 on the basis of 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. Belmaker (2017a) stressed that biogeographic reviews must clearly define 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. Dates and dating methods for major sites discussed in the text are provided in the online supplementary Table 1. 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 is also considered following Potts and Deino (1.2-0.7 Ma; 1995) to capture changes associated with the Middle Pleistocene Transition (MPT; ca. 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.

2. Middle Pleistocene fauna and its background

2.1 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*; however, recent excavations on Rusinga Island, Kenya, dated to the Late Pleistocene, unexpectedly yielded *Kolpochoerus* remains that closely match *K. majus* (Faith, 2014). This period also marked the arrival of the extant suids *Phacochoerus* and *Potamochoerus* in Africa. 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* was 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.

2.2 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 suggest, 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 ca. 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.

2.3 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).

2.4 Giraffidae

While restricted to Africa today, during the Mio-Pliocene giraffids were abundant in Eurasia and have been record 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 ca. 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 appears ca. 1 Ma at Bouri-Daka, Ethiopia (Asfaw et al., 2002). The only Middle Pleistocene non-African occurrences of *G. camelopardalis* are at Latamne, Syria (Guérin et al., 1993), and unidentified giraffid remains were found 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.

2.5 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 horn-core 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).

2.5.1 Hippotraginae

Hippotraginae are particularly well-adapted to arid conditions and are first known in Chad ca. 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).

2.5.2 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* arrived in the northern Saharo-Arabian region ca. 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.

2.5.3 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).

2.5.4 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 ca. 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.

2.5.5 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 identified ca. 400 ka at Doukkala II in Morocco (Michel and Wengler, 1993) and Lainyamok in Kenya (Faith et al. 2012; Potts & Deino 1995).

2.5.6 Bovinae

Bovinae inhabit a suite of habitats from grasslands (*Bos*) to wetlands and swamps (*Bubalus*). The earliest bovines remains are from the Siwaliks, India, and dated to around 8-9 Ma (Bibi, 2007). The first non-Oriental occurrences are noted from the UAE and Kenya and dated to 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* are noted at ‘Ubeidiya (Tchernov et al., 1994) and tentatively from Ti’s al Ghadah, Saudi Arabia (Thomas et al. 1998, but see below). *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 *Bo*s 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 P_4 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*.

2.5.7 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).

2.6 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, this 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).

2.7 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 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).

2.8 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, ca. 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, ca. 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, metapodial and astragalus remains of a large equid, similar in form to remains from Olduvai bed IV (dated ca. 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 in-situ 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).

2.9 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 ca. 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 ca. 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 ca. 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 ca. 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 younger occurrences of *P. recki*. Remains of *P. antiquus* have also been reported from Revadim, Israel (Marder et al., 1999).

2.10 Hyaenidae

Species of Hyaenidae were widely dispersed 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 ca. 1.2 Ma at Locality 642 and Locality 73 (Dennell et al., 2005a; 2005b), in Africa ca. 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 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 evidenced 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).

2.11 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.

2.12 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 ca. 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 dispersed into eastern Saharo-Arabia as evidenced by remains from Ti's al Ghadah, Saudi Arabia (Thomas et al., 1998; Stimpson et al., 2015). The fossils from Arabia mark the southernmost extent of this species (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*.

2.13 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'aqov 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.*

2.14 Mustelidae

Mustelidae arose in Eurasia during the Late Oligocene and 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 ʻUbeidiya, 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).

3. Late Pleistocene distribution

3.1 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).

3.2 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 ca. 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.

3.3 Camelidae

Like the Middle Pleistocene, the Late Pleistocene camelid record is scarce. Gautier (1966 and refereneces 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).

3.4 Bovidae

3.4.1 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 ca. 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 preservation biases of the Late Pleistocene. In Arabia, McClure (1984) reported *Oryx* remains from the Empty Quarter and it seems likely that they are *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 simply the Arabian Peninsula.

3.4.2 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).

3.4.3 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* sp. was identified from teeth and horn core remains recovered from the Empty Quarter and likely represents the extant and endemic *G. arabica* (McClure, 1984) and *G. gazella* and *G. subgutturosa* are known from Karaneh IV in Jordan (Martin et al., 2010) and Umm el Tlel in Syria (Griggo, 2004), respectively.

3.4.4 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 ca. 3.5 Ma, up until the Late Pleistocene. Notwithstanding this, reduncines are not found in the eastern Saharo-Arabian region during the Late Pleistocene.

3.4.5 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 that yielded 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

3.4.6 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.

3.4.7 Caprinae

Caprines were highly diverse and abundance 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 Quater, 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).

3.5 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.

3.6 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).

3.7 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), 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).

3.8 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 ca. 56 ka (Ghosh et al., 2016). Proboscideans have not been reported from Late Pleistocene deposits of the eastern Saharo-Arabia region.

3.9 Hyaenidae

Crocuta crocuta is known from all regions during the Late Pleistocene, although its remains in eastern Saharo-Arabia are known from only Wezmeh Cave, Iran (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).

3.10 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).

3.11 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). 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.

3.12 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).

3.13 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).

4. 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, speciation and migration that may have coincided with significant shifts in climate. Specifically, Vrba noted significant and rapid increases in the diversity and abundance of arid-adapted 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 ca. 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.

4.1 Biogeographical trends and turnovers

Faunal evidence indicates that there was little exchange between Africa and Eurasia between ca. 1.2 to 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 (ca.1.0-0.9 Ma) (Azzaroli, 1983; Azzaroli et al., 1988; Moullé et al., 2006). It is worth mentioning that the dispersal of *Theropithecus oswaldi* may have occurred around this time (Delson, 1993; Gilbert et al., 1995), however, tentatively assigned remains dated between 1.0-1.6 Ma are known from the Levant (Belmaker, 2002) and Italy (Rook et al., 2004). The extinction of the large *Pachycrocuta brevirostris* occurred around ca. 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 ca. 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 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). Interestingly, this period overlaps with dated sites from the Western Nefud in Saudi Arabia (Ti’s al Ghadah and Thomas loc-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 (Fig. 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, included *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 regions ca. 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 ca. 400-500 ka. Furthermore, at ca. 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.

The Palaearctic component in northwest Africa continued to 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 shifts in climate to the increased *Gazella* abundance in the Levant during the Late Pleistocene, 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. 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.

4.2 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 both the Middle and Late Pleistocene, Arabia experienced influxes of African, Palearctic and Oriental large mammals, and was also home to some endemics (*A. jayakari*, *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 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 presence of the large Eurasian endemic *P. gombaszogensis* at Ti's al Ghadah represents 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 very arid environments. They may have persisted elsewhere on the Arabian Peninsula during arid phases, perhaps making use of highland refugia (e.g. Yemeni highlands, 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.

4.3 Implications for hominin dispersal 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 ca. 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*, 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 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 gombaszogensis* and *E. hemionus* were likely novel taxa to hominins dispersing from Africa during the Middle Pleistocene, but overall, the taxonomic composition of Middle Pleistocene Arabia would be 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 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.

5. Summary

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 ca. 400-600 ka in Africa, with similar shifts in Levantine faunal assemblages during this period. It seems reasonable to suggest that climatic amelioration over the Arabian Peninsula, coupled with significant turnover in the surrounding regions, may have driven 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 (e.g. *Oryx leucoryx*). 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 have 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. Humans dispersing into Arabia from Africa (via the far south of the Levant), the northern Levant, or the Bab al-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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