



Middle Pleistocene vertebrate fossils from the Nefud Desert, Saudi Arabia: Implications for biogeography and palaeoecology



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ABSTRACT

The current paucity of Pleistocene vertebrate records from the Arabian Peninsula – a landmass of over 3 million km² – is a significant gap in our knowledge of the Quaternary. Such data are critical lines of contextual evidence for considering animal and hominin dispersals between Africa and Eurasia generally, and hominin palaeoecology in the Pleistocene landscapes of the Arabian interior specifically. Here, we describe an important contribution to the record and report stratigraphically-constrained fossils of mammals, birds and reptiles from recent excavations at Ti's al Ghadah in the southwestern Nefud Desert. Combined U-series and ESR analyses of *Oryx* sp. teeth indicate that the assemblage is Middle Pleistocene in age and dates to ca. 500 ka. The identified fauna is a biogeographical admixture that consists of likely endemics and taxa of African and Eurasian affinity and includes extinct and extant (or related Pleistocene forms of) mammals (*Palaeoloxodon* cf. *recki*, *Panthera* cf. *gombaszogenis*, *Equus hemionus*, cf. *Crocota crocuta*, *Vulpes* sp., *Canis anthus*, *Oryx* sp.), the first Pleistocene records of birds from the Arabian Peninsula (*Struthio* sp., *Neophron percnopterus*, *Milvus* cf. *migrans*, *Tachybaptus* sp. *Anas* sp., *Pterocles orientalis*, *Motacilla* cf. *alba*) and reptiles (*Varanidae/Uromastix* sp.). We infer that the assemblage reflects mortality in populations of herbivorous animals and their predators and scavengers that were attracted to freshwater and plant resources in the inter-dune basin. At present, there is no evidence to suggest hominin agency in the accumulation of the bone assemblages. The inferred ecological characteristics of the taxa recovered indicate the presence, at least periodically, of substantial water-bodies and open grassland habitats.

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1. Introduction

The Arabian Peninsula (defined here as the landmass from the southern borders of Iraq and Jordan, to the southern coastline of Yemen; Fig. 1A) is a key theatre to consider hominin dispersals between Africa and Eurasia (e.g. Rose and Petraglia, 2009; Dennell and Petraglia, 2012; Groucutt and Petraglia, 2012). While the

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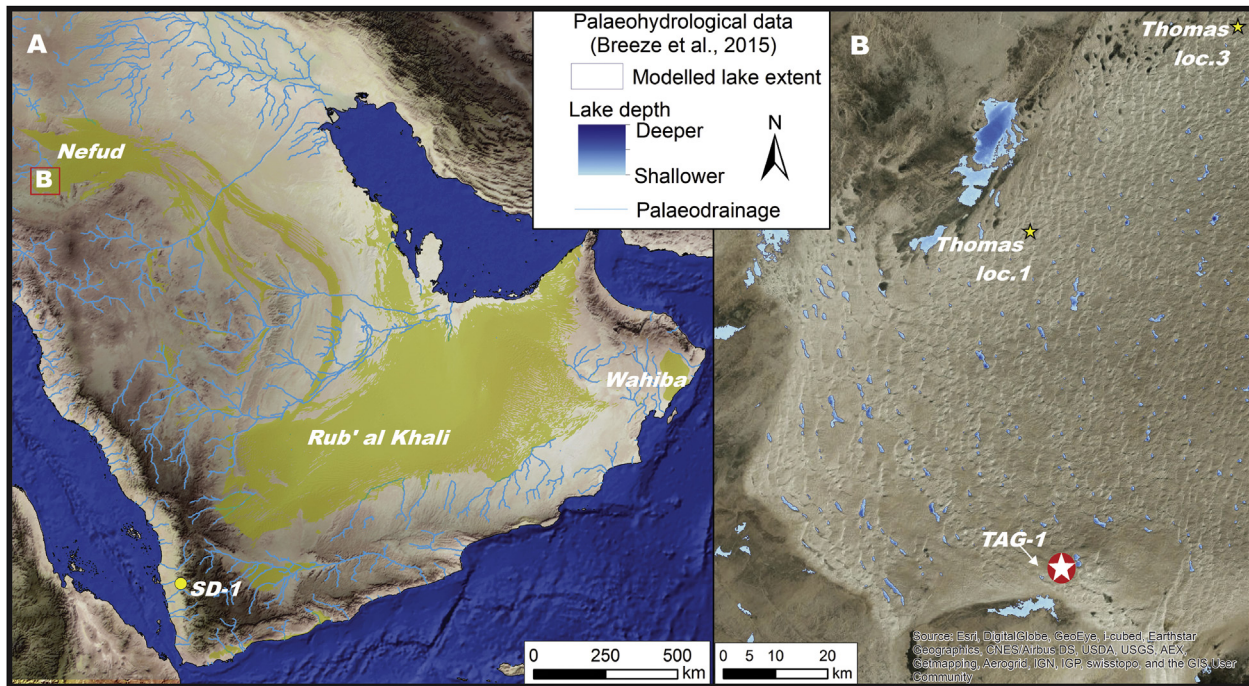


Fig. 1. A: The Arabian Peninsula, showing locations of three major sand seas and the site of Shi'bat Dihya (SD-1) and B: Southwestern Nefud Desert showing location of Ti's al Ghadah (TAG-1) and other Thomas et al. (1998) fossil sites.

geographical significance of this landmass of over 3 million km² as a link between these continents is self-evident, the potential routes and timing of dispersals and exchange by animals and hominins in the Pleistocene (2.6 Ma–0.011 Ma) are much-debated (e.g. O'Regan et al., 2005; Beyin, 2006; Fernandes et al., 2006; Fernandes, 2009; O'Regan et al., 2011; Groucutt et al., 2015a).

As studies continue to unveil a complex climatic and environmental history (e.g. Fleitmann et al., 2003; Fleitmann and Matter, 2009; Parker, 2009; Fleitmann et al., 2011; Rosenberg et al., 2011, 2013; Breeze et al., 2015; Jennings et al., 2015; Matter et al., 2015; Parton et al., 2015a, 2015b) and the Palaeolithic archaeological record develops (e.g. Armitage et al., 2011; Delagnes et al., 2012; Groucutt and Petraglia, 2012; Petraglia et al., 2012) it is now clear that Pleistocene hominins penetrated the interior of the Peninsula (Groucutt et al., 2015b, 2015c; Shipton et al., 2014; Scerri et al., 2015) in regions that are today harsh, hyper-arid habitats. A key line of evidence to contextualise these movements is, however, lacking: stratigraphically- and chronologically-constrained records of vertebrates. Here, we describe an important step towards addressing this issue.

North Africa and the Middle East are biogeographically complex regions. The Arabian Peninsula is situated at the junction of three biogeographic realms, the Afrotropical, Western Palearctic and Oriental (e.g. Portik and Papenfuss, 2012) and the historical vertebrate fauna is an admixture of endemic species with taxa of African and Eurasian affinity (e.g. Delany, 1989; Harrison and Bates, 1991; Cox et al., 2012; Portik and Papenfuss, 2012). The opening of the Red Sea and climatic shifts in the late Miocene were major drivers of diversification and dispersal of the biota of the region and a combination of harsh arid environments, periodic humid events and geological evolution has shaped the fauna of the Peninsula (e.g. Metallinou et al., 2012). Genetic studies of a small number of species (*Papio hamadryas*, *Ichneumia albicauda* and *Varanus yemenensis*) have shed light on the biogeographical history of aspects of the regional Pleistocene fauna (Fernandes, 2009, 2011 and Kopp

et al., 2014; Portik and Papenfuss, 2012, respectively) but, in contrast to works on Miocene vertebrates (e.g. Whybrow and Hill, 1999; Beech and Hellyer, 2005), the paucity of Pleistocene records from the Arabian Peninsula remains a major limiting factor in modelling the dynamics of Quaternary animal populations (e.g. Fernandes, 2009; O'Regan et al., 2011; Stimpson et al., 2015). Furthermore, while records of vertebrate taxa cannot be considered as direct or unequivocal proxies for the dispersal of hominins (e.g. Bar-Yosef and Belmaker, 2011) and species responses to climatic and environmental changes are individualistic (e.g. Stewart, 2009), such data are critical lines of contextual evidence in considering Pleistocene environments and hominin palaeoecology in the interior (e.g. Belmaker, 2009).

The Arabian Peninsula today comprises of a heterogeneous suite of habitats, including tropical, sub-tropical and montane biomes in the south and western coastal regions. The interior, however, is dominated by basalt flows, salt flats and (overwhelmingly) sand and gravel deserts (Mallon, 2011; Cox et al., 2012). These hyper-arid habitats are embodied by three major sand seas that collectively occupy over 700,000 km²: the Rub' al Khali (also known as the Empty Quarter) and Wahiba Sands in the south and southeast, respectively, and the Nefud Desert in the north (Fig. 1A). During the Pleistocene, oscillations between hyper-arid and humid conditions saw periodic increases in precipitation, humidity and the activation of river and lake systems in the interior (Parker, 2009; Rosenberg et al., 2013; Breeze et al., 2015; Matter et al., 2015; Parton et al., 2015b, Fig. 1A, B). As the volume and periodicity of available moisture increased plant biomass will have responded accordingly (e.g. Southgate et al., 1996) and an availability of fresh water resources would have led to a "greening" of the interior that in turn would have provided windows of opportunity for dispersal for animals and hominins (e.g. Parton et al., 2015a). However, the character and composition of the animal populations of these landscapes is poorly known. The existing collections of Pleistocene fossils have provided taxonomic insights (Table 1) but are beset by

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