

Tabula rasa or refugia? Using genetic data to assess the peopling of Arabia

This paper provides a broad overview of the current state of archaeogenetic research in Arabia. We summarise recent studies of mitochondrial DNA and lactase persistence allele -13915*G in order to reconstruct the population histories of modern Arabs. These data, in turn, enable us to assess different scenarios for the peopling of the Peninsula over the course of the Late Pleistocene and Early Holocene. The evidence supports the posited existence of Arabian refugia, although it is inconclusive which (e.g. Persian Gulf basin, Yemeni highlands and/or Red Sea basin) was/were responsible for housing ancestral populations during the Last Glacial Maximum. Synthesising genetic and archaeological data sets, we conclude that a substantial portion of the present South Arabian gene pool derives from a deeply rooted population that underwent significant internal growth within Arabia some 12,000 years ago. At the same time, we interpret the disappearance of Nejd Leptolithic archaeological sites in southern Arabia around 8000 years ago to represent the termination of a significant component of the Pleistocene gene pool.

Keywords: archaeogenetics, mitochondrial DNA, lactase persistence, Late Palaeolithic, Arabian demographics, refugia

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Introduction

Alternative scenarios have been proposed to explain the relatively sudden proliferation of human settlements throughout the Arabian Peninsula, which occurred during the Early Holocene, between 10,000 and 8000 years ago (ka BP). The ‘Levantine Expansion’ envisions a migration of Pre-Pottery Neolithic B (PPNB) pastoralists from the Levant¹ (e.g. Drechsler 2007; Uerpman *et al.*, 2009), while the ‘refugia’ model argues for the spread of indigenous groups within Arabia itself (e.g. Bailey 2009; Fedele 2009; Rose 2010). These opposed hypotheses are built on diverging premises regarding the habitability of the Arabian Peninsula during the Last Glacial Maximum (LGM) that culminated around 20 ka BP. In the former scenario, hyper-arid conditions are thought to have caused a demo-

graphic *tabula rasa* that effectively wiped out all of the Pleistocene populations in the Peninsula, while the latter scenario proposes that some groups survived in environmental refugia. In this paper, we review the state of archaeogenetic research, focusing on the mitochondrial DNA (mtDNA) and lactase persistence (LP) diversities of modern Arabian populations. These data are used to assess the peopling of Arabia. We consider this evidence in respect to recent archaeological findings throughout the Peninsula.

Environmental setting

The Arabian Peninsula comprises diverse habitats governed by topography and differing climatic regimes. The southern part of the Peninsula is fed by summer rainfall brought by the Indian Ocean monsoon, while the northern and eastern portions are watered by winter cyclones from the eastern Mediterranean. High elevations in the mountains of western Yemen and across the Dhofar escarpment

¹ For the purposes of this paper, the term ‘Levant’ refers to the eastern Mediterranean region, ‘Near East’ encompasses a broader area of the Levant, northern Arabia and Mesopotamia, and ‘southern Arabia’ is the portion of the Peninsula lying south of (and including) the Rub’ Al Khali.

act as orographic barriers, trapping moisture from the monsoon (Fig. 1). It is noteworthy that much of southern Arabia forms an extension of the East African Somali-Masai and Saharo-Sindian phytogeographic zones, while elsewhere the Peninsula is primarily home to Eurasian Palaeartic plant species (Ghazanfar & Fisher 1998).

Episodic climate change over the course of the Late Pleistocene (*c.* 130–10 ka BP) had a profound effect on the landscapes of Arabia (for summaries of climatic proxy evidence see Parker & Rose 2008; Fleitmann *et al.* 2011). During pluvial phases, deserts were transformed into savanna grasslands, lakes and aquifers were recharged and drainage systems were activated. Arid phases triggered widespread desertification; while at the same time, reduced sea levels exposed several hundred thousand square kilometres of land in the Persian Gulf and Red Sea basins (Bailey 2009; Rose 2010). Due to the availability of fresh water in the form of upwelling springs along exposed continental shelves (Faure, Walter & Grant 2002), the Gulf Oasis, south-east Arabian littoral zone and Red Sea basin may have served as significant demographic refugia. WorldClim rainfall models show that the mountains of western Yemen, reaching over 3000 m in elevation, could have continued to produce as much as

600 mm of rainfall per year during the LGM (Hijmans *et al.* 2005).

The habitability of these hypothetical refugia over the course of the Late Pleistocene remains speculative. One means of indirectly evaluating this prospect is through an examination of the genetic structure among modern inhabitants of Arabia, particularly in the south of the Peninsula, in and around the supposed refugia.

Mitochondrial DNA

Modern groups throughout Arabia show a high frequency of mtDNA haplogroup R0a² (Kivisild *et al.* 2004; Abu-Amero *et al.* 2007). Analysis of R0a sequences recorded in Saudi Arabia exhibit a relatively low incidence of ancestral motifs and considerable overlap with surrounding areas such as the Near East and East Africa. This initially led researchers to consider Arabia as a demographic dead end — a sump in the gene pool fed by adjacent population centres (Cabrera *et al.* 2009). More recently, however, analyses of R0a sequences throughout Yemen and Dhofar have documented a number of haplotypes unique to South Arabia (Fig. 2/a) (Černý *et al.* 2008, 2009, 2011; Al-Abri *et al.* 2012a). This haplogroup is also common among the people of Soqatra Island, located some 350 km off the southern coast of Yemen, where it is both the most frequent and most diverse type observed (Černý *et al.* 2009).

A robust phylogenetic tree comprising eighty-nine whole genome R0a sequences shows three branches with different age estimates. The oldest, R0a1, appears to diverge from ancestral R0a at approximately 22 ka BP.³ After that, the R0a2 and R0a3 branches coalesce immediately following the LGM, around 15 and 12 ka BP, respectively. Given these age estimates, and later coalescence times in the Saudi Arabian R0a variants (Abu-Amero *et al.* 2007), evidence suggests that only the southern portion of the Peninsula was occupied by R0a lineages

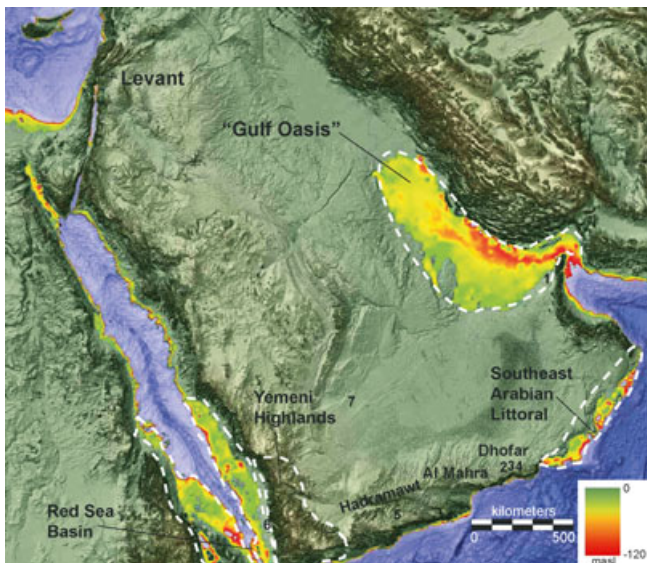


Fig. 1.

Map of Arabia showing proposed demographic refugia, regional names and specific archaeological sites mentioned in the text. 1. Jebel Faya; 2. Khamseen rock shelter; 3. Ghazal rock shelter; 4. Al Hatab rock shelter; 5. Manayzah rock shelter; 6. Wadi Surdud site complex; 7. Al Faw Well site.

² Formerly referred to as (preHV)1, see Torroni *et al.* 2006 for reclassification.

³ For this and all other mtDNA coalescence dates presented in this paper, we stress the uncertainty of genetic dating. These are estimates contingent upon different statistical models and assumptions. The dates and ranges we present are certain to be refined as the field of archaeogenetics continues to develop. Nevertheless, molecular coalescence dating has undergone intense study in the last decade and provides useful chronological markers that can be further calibrated through synthesis with archaeological data.

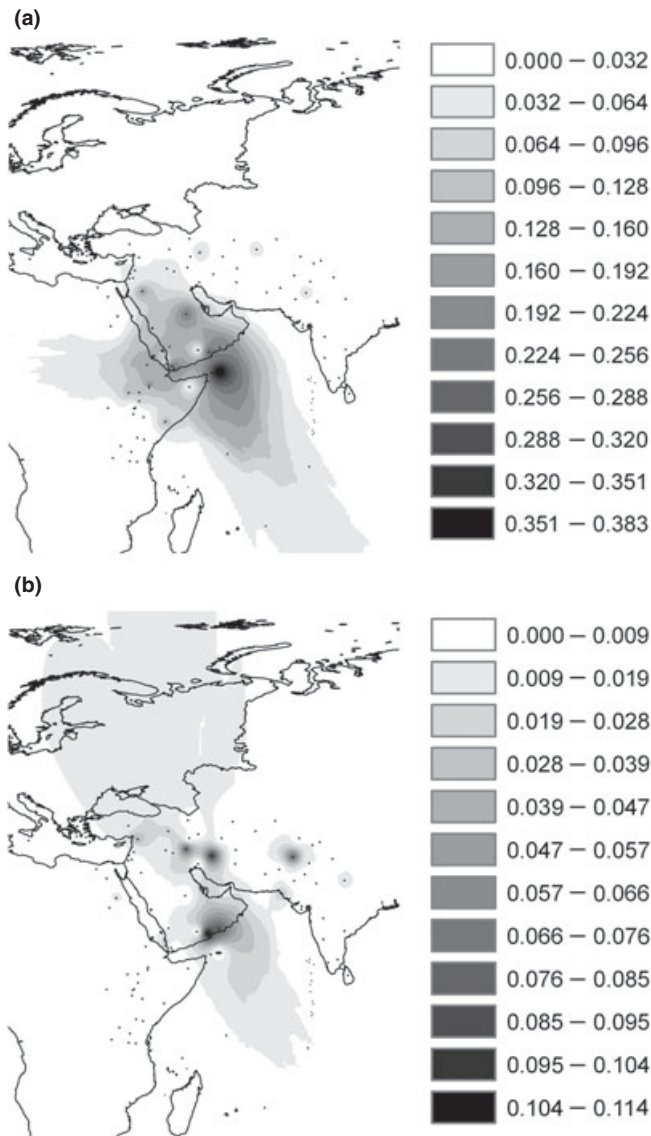


Fig. 2. Interpolation maps for the frequency distribution of: **A.** haplogroup R0a and **B.** haplogroup R2 in the Arabian Peninsula and surrounding territories.

during the LGM. At the same time, while cut off from the north, there appears to have been demographic exchange between South Arabia and East Africa (particularly Ethiopia). Subsequent internal expansions within Arabia began at the onset of the Holocene, signalled by age estimates on several younger clades such as R0a1a1, R0a1a4, R0a2a and R0a2c. There are only two R0a daughter lineages (R0a1a1a and R0a2f1) that diverge after 5 ka BP, at which time the climate grew increasingly arid. These clades are specific to eastern Yemen, southern Oman and the island of Soqatra (Černý *et al.* 2011).

Unlike R0a, which is specific to southern Arabia, HV1 is more commonly found in East Africa, the greater Near East and North Africa. Phylogeographic inference suggests this haplogroup arose in the Levant around 22 ka BP; we have detected its subsequent diversification in Yemen by 15 ka BP. Two daughter branches are distributed across both Yemen and East Africa, which diverge *c.*10 (HV1b1) and *c.*7 ka BP (HV1a3), posited to be the result of ancient maritime interaction (Musilová *et al.* 2011).

Haplogroup R2 is overwhelmingly concentrated in southern Arabia (Fig. 2/b), where its distribution is found to be congruent with Modern South Arabian language speakers. Although this haplogroup has been observed sporadically throughout the greater Near East, the frequency of R2 rises significantly among semi-sedentary communities distributed in Yemen and southern Oman. Moreover, like R0a, R2 shows higher internal diversity among populations in southern Arabian than anywhere else. Analysis of whole genome R2 sequences in Dhofar and Al Mahra indicates that it arose locally and began spreading to the rest of the Peninsula around 13 ka BP (Al-Abri *et al.* 2012a).

Lactase persistence allele -13915*G

Further evidence for the distinctive origin of present-day people in southern Arabia is provided by the distribution, frequency and ancestral haplotype background of lactase persistence (LP) -associated allele -13915*G (Imtiaz *et al.* 2007; Tishkoff *et al.* 2007; Enattah *et al.* 2008; Al-Abri *et al.* 2012b). The global spread of lactase persistence within the last 10,000 years is directly linked to animal domestication, by creating selective pressures favouring those individuals able to digest lactose (i.e. milk sugar) into adulthood. This particular allele, closely correlated with the modern population of the Arabian Peninsula, is found in high frequencies among Saudi Arabs, Yemenis and Dhofaris (Fig. 3). Its significantly lower frequencies or absence in neighbouring parts of the Near East, Iran and Pakistan, as well as the absence of the other major European LP variant allele -19310*T, suggests that the -13915*G mutation is rooted within the Peninsula.

The epicentre of LP -13915*G distribution in the Arabian Peninsula is among the people of Dhofar (Al-Abri *et al.* 2012b), which is most likely the result of either selective pressure or genetic drift. The distribution of the -13915*G allele demonstrates clinal decrease within the Arabian Peninsula and neighbouring areas. The moderate

to high prevalence among Saudi Arabs is due to the more recent migrations from Yemen and Hadramawt to the north over the past 3000 years.

The two major global LP mutations, -13910*T and -13915*G, have entirely different ancestral haplotype backgrounds; hence, they appear to have arisen independently due to strong selective pressure driven by different animal domestication processes (Enattah *et al.* 2008). While -13915*G prevails in Arabia and East Africa, -13910*T occurs in the northern part of western Eurasia (excluding Arabia) and in north-western Africa (Enattah *et al.* 2008; Al-Abri *et al.* 2012b). We also observe that the distribution of LP variant allele -13915*G is congruent with the distribution of mtDNA haplogroup R0a.

Although faunal preservation in Arabia is quite rare and little is known of prehistoric subsistence strategies, the earliest indication of pastoralism in Arabia comes from the Manayzah rock shelter in Yemen. The faunal assemblage, dated to *c.* 8 ka BP, shows a combination of gazelle and domesticated sheep, goat and cattle, suggesting a mixed economy of hunting and herding (McCorrison & Martin 2009). The excavators conclude, 'the Manayzah dates and lithics do not point to an introduction of pastoral economies or people closely related either in time or in material culture to the Levantine PPNB' (2009: 247–248).

The geographic distribution of LP-associated allele -13915*G adds some credence to the authors' suggestion that the transition from hunting and gathering to pastoralism might have been a local developmental process within southern Arabia, and not the result of population migration. This proposition, however, will require more data and more stratified and dated sites with domesticated fau-

nal remains to be verified. It is not yet known whether the livestock themselves are derived from Near Eastern domesticates, or descend from wild progenitors within southern Arabia (e.g. Cattani & Bökönyi 2002). In the case of Jebel Buhais 18 in Sharjah, UAE, ancient DNA extracted from a 7000-year-old cattle bone indicates a general Near Eastern origin for domesticated livestock at the site (Uerpmann & Uerpmann 2008). It should be noted that the Near East, in this case, potentially encompasses the Levant, Anatolian plateau, Mesopotamia, Arabian Peninsula and Taurus-Zagros mountain ranges — throughout all of which *Bos primigenius* once ranged in the Late Pleistocene.

Late Pleistocene archaeology

If human groups expanded onto the Peninsula in periods predicted by mtDNA analyses, it is reasonable to hypothesise that toolmakers brought with them the lithic technology from whence they came. Although derived forms of a lithic tradition might change somewhat in new demographic and environmental circumstances, these would retain at least some ancestral character, as lithic reduction is a learned, hence cultural, behaviour.

The earliest indications for modern human groups in the Arabian Peninsula come from the sites of Jebel Faya in Sharjah, UAE, and a constellation of sites found in Hadramawt and Dhofar belonging to the Afro-Arabian Nubian technocomplex. The latter is attributed, by some researchers, to the expansion of hunter-gatherers from the Nile Valley around 100 ka BP (Rose *et al.* 2011; Usik *et al.* 2012), while excavators of Jebel Faya have suggested the site represents a population from East Africa that moved into Arabia and settled around the Persian Gulf 130 ka BP (Armitage *et al.* 2011). Given the potential role of the Gulf Oasis as a population refugium, it is significant that the upper archaeological levels at Jebel Faya, loosely bracketed between 95 and 35 ka BP, are interpreted as an autochthonous lithic industry unrelated to the surrounding areas (Marks 2009; Armitage *et al.* 2011). In southern Arabia, the Mudayyan industry has been argued to represent a stage of technological development subsequent to, and derived from, the classic Dhofar Nubian industry (Usik *et al.* 2012).

At the Wadi Surdud site complex, situated at the interface of the Tihama plain and Yemeni highlands, several thousand lithic artefacts were dated between 63 and 42 ka BP (Delagnes *et al.* 2012; Sitzia *et al.* 2012). The assemblages, found interstratified within a 6 m fluvial accretion,

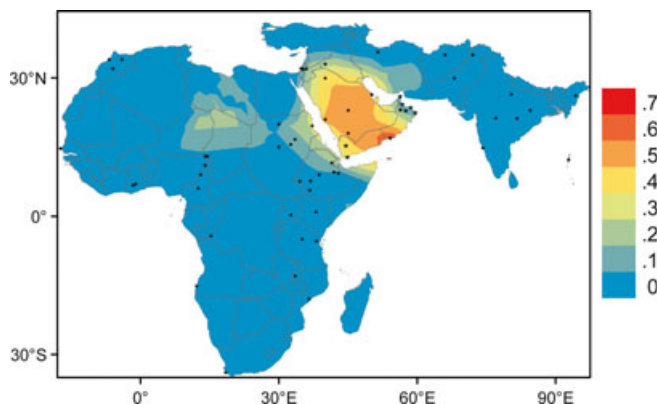


Fig. 3. Interpolation map for the frequency distribution of lactase persistence associated allele -13915*G in the Arabian Peninsula and surrounding territories.

are assigned to the Middle Palaeolithic and are characterised by a combination of occasional Levallois and, more frequently, non-Levallois convergent laminar reduction strategies accompanied by a low percentage of informal tools. Pointing out broad similarities with the Levantine Mousterian, the authors interpret the evidence from Wadi Surdud as uniquely Arabian — only vaguely resembling coeval Levantine technologies and having no overlap whatsoever with East African Middle Stone Age sites.

There are no archaeological sites in Arabia between 30 and 20 ka BP within which mtDNA R0a's most recent common ancestor is supposed to have diverged. If human groups spread southwards from the Levant during this phase, we might expect to find lithic technologies resembling the Levantine Late Ahmarian — a volumetric blade (let) industry distinguished by the removal of crested blades and core tablets to prepare and maintain the core. Diagnostic tools associated with this industry include pointed and retouched blade(lets), Ouchtata blade(lets), end scrapers, burins and non-geometric microliths (Gilead 1991). No such features have been found in southern Arabia.

The Nejd Leptolithic levels of Al Hatab rock shelter in Dhofar are bracketed between 15 and 10 ka BP (Rose & Usik 2009), while nearby Ghazal and Khamseen rock shelters yielded dates between 10 and 8 ka BP (Hilbert, Rose & Roberts 2012). These sites exhibit similar lithic assemblages, characterised by the volumetric unipolar-parallel and unipolar-convergent production of blade blanks for the manufacture of Fasad points, burins, end scrapers, side scrapers and perforators. This techno-typological package is assigned to the Nejd Leptolithic regional tradition, the antiquity of which has yet to be established. Of additional concern, the date ranges described from the Dhofar rock shelters may only indicate the time at which these assemblages were buried — a *terminus post quem* — rather than when the artefacts were manufactured.

Thousands of technologically homologous, laminar-based lithic assemblages have been documented across southern Arabia (e.g. Rose 2002, 2006; Amirkhanov 2006; Crassard 2008; Rose & Usik 2009; Hilbert 2012). It is ambiguous, however, whether these belong to a single lithic tradition that persisted from *c.*50 to *c.*10 ka BP, or represent coincidental reinventions of the same technological process. Both Rose and Usik (2009) and Hilbert (2012) classify these sites within a single 'Late Palaeolithic' technocomplex, envisioning cultural continuity in Dhofar and the Yemeni highlands during the latter half of the Late Pleistocene. On the other hand, there are fundamental differences between Wadi Surdud and Nejd Leptolithic

assemblages: in the former instance, blade production is but one component among a variety of reduction strategies, while Nejd Leptolithic assemblages exclusively exhibit blade manufacture. In either case, it seems that the Nejd Leptolithic tradition was replaced in Dhofar by a technologically disparate lithic industry sometime around 8 ka BP. This cultural 'replacement' is exemplified in the shift from Late Palaeolithic to Neolithic cultural horizons at Khamseen rock shelter (Hilbert, this volume).

Finally, the 'pre-Neolithic' levels from the site of Wadi Thayilah provide hints of human occupation in the Yemeni Highlands prior to the onset of the Holocene (Fedele 2009); the small lithic assemblage from the site, however, is non-diagnostic and does permit comparison with material found elsewhere.

Discussion

We reject a strict *tabula rasa* scenario in favour of the Arabian refugia hypothesis. While the LGM may have caused a severe demographic bottleneck, genetic evidence indicates that it did not lead to complete depopulation of the Peninsula. The geographic source of these pre-LGM populations in Arabia cannot yet be determined, only that they are closely linked to the greater Near Eastern gene pool. The disappearance of the Nejd Leptolithic may represent the termination of a sizable pre-Holocene population and explain the absence of more deeply rooted haplotypes among modern Arabs.

Haplogroup R0a is among the most frequent in South Arabia, diverging from a common Near Eastern ancestral population around 22 ka BP. The demographic source of this expansion is unresolved. No contemporary Levantine cultural features (i.e. Late Ahmarian or Geometric Kebaran) are found in southern Arabia; hence, we remain open to the possibility of other Near Eastern source areas for R0a, such as Mesopotamia, the Gulf Oasis or even a local origin in the Yemeni highlands. The major diversification of R0a in Arabia occurred after the LGM. Again, archaeological evidence does not support demographic input from the Levant, as there are no Epipalaeolithic sites or shared technological features present in southern Arabia.

The hypothesis of a Levantine PPNB expansion, as it pertains specifically to southern Arabia, is supported by neither genetic nor archaeological data. Distinct cultural features of the PPNB such as naviform core technology, sickle segments, architecture, portable art, interred plastered skulls and plant processing are absent in southern Arabia. Although the South Arabian and Near Eastern

gene pools are distantly related, their divergence is likely to have occurred long before the appearance of hunter-herder populations in Arabia. Moreover, both archaeological and genetic LP evidence hint at an autochthonous origin of pastoralism in southern Arabia.

In sum, we observe the peopling of Arabia to have been an amalgamation of internal demographic events coinciding with post-glacial climatic cycles. As Uerpmann, Potts and Uerpmann (2009: 14–15) suggest, ‘...the situation may be far more complex than previously assumed, and that it is wrong to speak of “colonization” in the singular.

It is unlikely to have been an “event” either, and much likelier to have been a process which may initially have involved hunters and gatherers coming from the south...’ Archaeogenetics corroborate this proposition, showing a significant portion of the modern Arabian gene pool comes from indigenous, pre-Holocene inhabitants. From the widespread disappearance of Nejd Leptolithic assemblages across southern Arabia around 8 ka BP, we surmise that the current mtDNA variability represents but a small fraction of the Pleistocene lineages that once occupied the Peninsula.

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