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Contents

Palaeogenomics and the Palaeolithic of Southwest Asia: Trends, Issues, and Future Directions

David L. G. Miedzianogora

Abstract

Palaeogenomics is the study of ancient subfossilised remains on a genome-wide level, and it has revolutionised the study and understanding of the deep past. This is also the case in Southwest Asia, where especially the Bronze and Iron Ages have seen substantial research. However, due to the poor preservation of DNA in the region, the Palaeolithic remains largely understudied despite the possibility of novel interpretations of this key period. Here, I review several ways that palaeogenomics has begun changing our understanding of the Palaeolithic of the region in three key areas: the dispersal of modern humans out of Africa, the interactions between Neanderthals and modern humans, and the formation of Southwest Asian population structures. Most of these interpretations are based on data from outside of Southwest Asia, and I argue that a closer integration between palaeogenomics, archaeology, and local stakeholders are necessary to begin solving the issues surrounding the poor preservation of DNA in the region. If this can be done, palaeogenomics holds many possibilities for future Palaeolithic research.

علم الجينوم القديم هو دراسة بقايا المحفوظات القديمة جزئيًا المتحجرة على مستوى الجينوم، وقد غير هذا العلم دراسة وفهم الماضي العميق. وهذا األمر ينطبق أيًضا على جنوب غرب آسيا، حيث شهدت العصور البرونزية والحديدية بحًثا مكثًفا كبيًرا. ومع ذلك، نظًرا لسوء حفظ الحمض النووي في المنطقة، فإن بقايا العصر الحجري القديم لم تدرس بشكل كبير على الرغم من إمكانية تفسيرات جديدة لهذه الفترة الحاسمة. في هذه المقالة، سأستعرض عدة طرق بدأ فيها علم الجينوم القديم في تغيير فهمنا للعصر الحجري القديم في المنطقة في ثالثة مجاالت رئيسية: انتشار البشر الحديثين من أفريقيا، والتفاعالت بين النياندرتال والبشر الحديثين، وتشكل هياكل السكان في جنوب غرب آسيا. معظم هذه التفسيرات مبنية على بيانات من خارج جنوب غرب آسيا، وأقدم حجة بأن التكامل األكثر قرًبا بين علم الجينوم القديم واآلثار والجهات المعنية محلًيا ضروري لبدء حل لمشكالت المتعلقة بسوء حفظ الحمض النووي في المنطقة. إذا تم ذلك، فإن علم الجينوم القديم يحمل العديد من اإلمكانيات لبحوث العصر .الحجري المستقبلية

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Introduction

The ability to extract and sequence ancient DNA (aDNA) from archaeological organic remains on a genome-wide level has opened up novel ways of interrogating the deep past (Orlando et al. 2021). It has led to the burgeoning of a new field, palaeogenomics, which has begun untangling the evolutionary history of past human populations at the broad and local scale, and it has been depicted as an integral part of "The Third Science Revolution" in archaeology (Kristiansen 2014). Its importance has been particularly felt in Europe, where most studies have been conducted so far (e.g., Haak et al. 2010; Brandt et al. 2013), but it is prone to revolutionise the study of prehistory everywhere (e.g., Narasimhan et al. 2019). This is also the case of Southwest Asia, where the application of palaeogenomics can help develop our understanding of several key questions in human prehistory.

Nevertheless, several issues persist for the field in Southwest Asia: First, palaeogenomic studies from the region itself are rare, and those that have been conducted tend to focus on the region as a means of understanding the prehistory of Europe rather than the demographic processes within the region itself (Gokcumen and Frachetti 2020). Second, researchers have highlighted the lack of equal research collaborations with key stakeholders outside the Global North (e.g., Wagner *et al.* 2020; Alpaslan-Roodenberg et al. 2021; Somel et al. 2021; Ávila-Arcos *et al.* 2022), which applies to Southwest Asia as well. Finally, the lack of proper engagement with archaeological and anthropological data and methods in most palaeogenomic studies has been criticised (Horsburgh 2015; Heyd 2017). These issues can be solved by initating ethically founded frameworks aimed at ensuring closer collaboration between palaeogenomics and other fields of human prehistory to ensure that data are produced and interpreted ethically and collaboratively (Gokcumen and Frachetti 2020; Veeramah 2018; Furholt 2018). To accomplish this task in Southwest Asian archaeology, researchers first need a better understanding of the way that palaeogenomics can be applied constructively to archaeological research in the region.

This article seeks to review some of the key ways in which palaeogenomic data can be used to answer archaeological questions and transform current interpretations of the Palaeolithic of Southwest Asia. Due to its central location as the landbridge between Africa, Asia, and Europe, the region is key for understanding major questions in human prehistory beginning with the first dispersal of hominins out of Africa more than 2 million years (Ma) ago (Ronen 1991; Gabunia *et al. 2000;* Ferring *et al.* 2011; Zhu *et al.* 2018*;* Scardia *et al.* 2019; 2021). Nevertheless, the bulk of studies from the region have sequenced genomes belonging to individuals postdating the Neolithic (Fig. 1), with the oldest sequenced genome dating to 26 thousand years (ka) old (it remains in preprint; Lazaridis *et al.* 2018), whilst the oldest published genome dates to 15 ka (Feldman et al. 2019), highlighting the dearth of Palaeolithic genomes from the region. Consequently, most reviews have focused on the impact

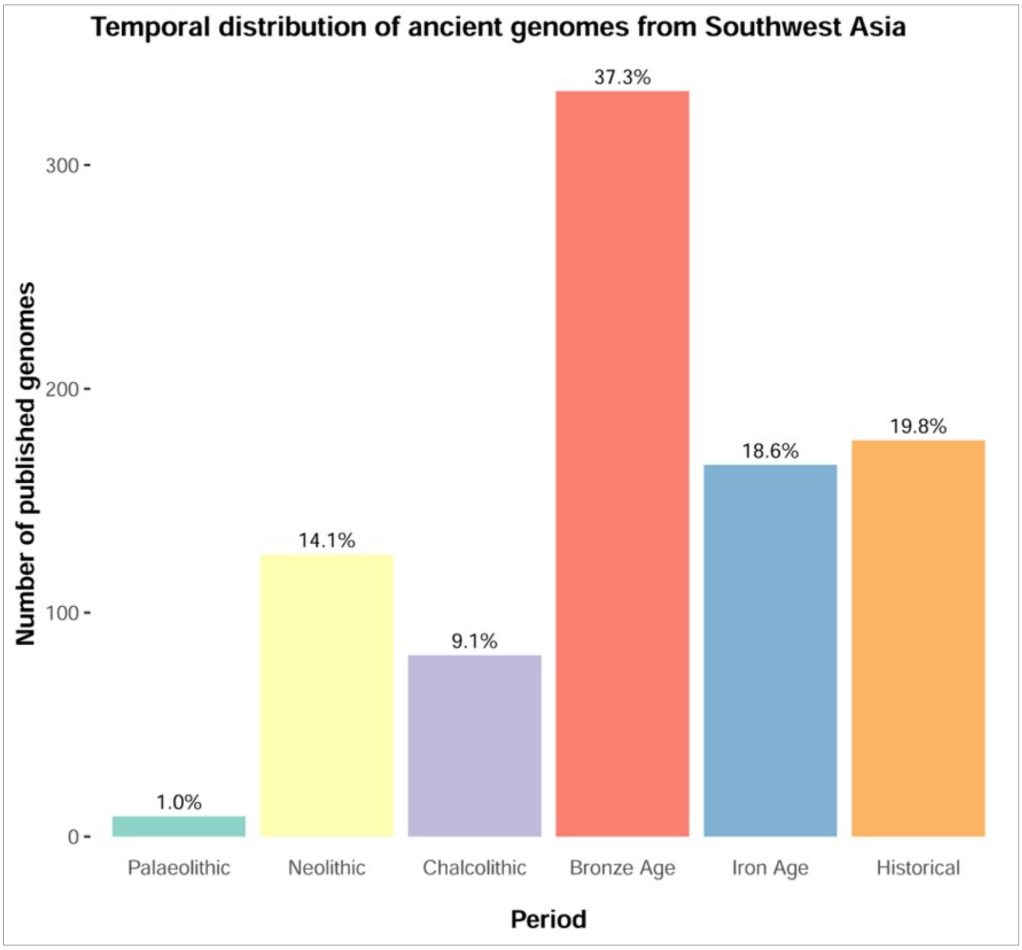


Figure 1: Temporal distribution of published genomes (n = 1042) from Southwest Asia as of September 2023, based on data from Mallick and Reich (2023) and Mallick *et al.* (2023). From the left: Palaeolithic, teal (>11,500 cal. BP), Neolithic, yellow (11,499-6,950 cal. BP), Chalcolithic, purple (6,949-5,250 cal. BP), Bronze Age, red (5,249-3,150 cal. BP), Iron Age, blue (3,149-2,500 cal. BP), and Historical, orange, (<2,499 cal. BP). All dates are mean dates. Modern and duplicate genomes have been removed from the dataset. Produced by author in R version 4.3.2 (2023) using the Tidyverse package (Wickham *et al.* 2019). Dataset available as Suppl. Dataset 1 at tidsskrift.dk/chronolog, R code available upon request.

of palaeogenomics for the Neolithic and historical periods (Broushaki *et al.* 2016; Omrak *et al.* 2016; Olalde and Posth 2020; Skourtanioti *et al.* 2020). The focus of this article is instead on the impact that palaeogenomic data has had on three key areas in the Palaeolithic of Southwest Asia: the dispersal of modern humans (*Homo sapiens*) out of Africa, the interactions between Neanderthals (*Homo neanderthalensis*) and modern humans in the Levant, and the formation of Palaeolithic population structures throughout Southwest Asia. These issues are not only relevant for Southwest Asian prehistory but also for understanding broader issues in palaeoanthropology and palaeolithic archaeology. Interpretations remain tentative, however, and more genetic data is needed directly from the region to test current hypotheses. How best to achieve this remains an open question, however, and some possible paths forward are suggested here. The methods and theories of palaeogenomic analysis have been reviewed thoroughly elsewhere (e.g., Jobling *et al.* 2004; Pedersen *et al.* 2015; Orlando *et al.* 2021; see also Jones and Bösl 2021), hence they are not discussed in this article.

Out of Africa and into Eurasia

Although the exact timing and mode of appearance of anatomically modern humans in Africa is contested, it is generally agreed that our species evolved ~300,000 ka based on a combination of fossil, archaeological, and genetic evidence (reviewed in Bergström *et al.* 2021). Dating the dispersal of modern humans out of Africa has proven more difficult. Genetics from modern populations suggest that all non-Africans derive from a migration 60-70 ka ago (Underhill and Kivisild 2007; Soares *et al.* 2012; *Malaspinas et al.* 2016; Mallick *et al.* 2016; Nielsen *et al.* 2017; Bergström *et al.* 2020; but see Pagani *et al.* 2016), yet the earliest fossil evidence of modern humans outside Africa is 210 ka old from Greece (Harvati *et al.* 2019). Some researchers contest this fossil, which consists solely of fragmented parts of a posterior cranium, which, depending on how it is reconstructed, might also cluster with Neanderthal features (see de Lumley *et al.* 2020; Rosas and Bastir 2020). Less contested is a slightly younger maxilla from Misliya Cave in the Levant, dated to 180 ka (Hershkovitz *et al.* 2018; but see also Sharp and Paces 2018). Palaeoenvironmental reconstructions show that both the Nile-Sinai Valley and the Bab el-Mandeb Strait were crossable during several windows throughout the past 400 ka, highlighting the possibility of continuous dispersals into Southwest Asia beginning soon after the appearance of modern humans in Africa (Tierney *et al.* 2017; Beyer *et al.* 2021;

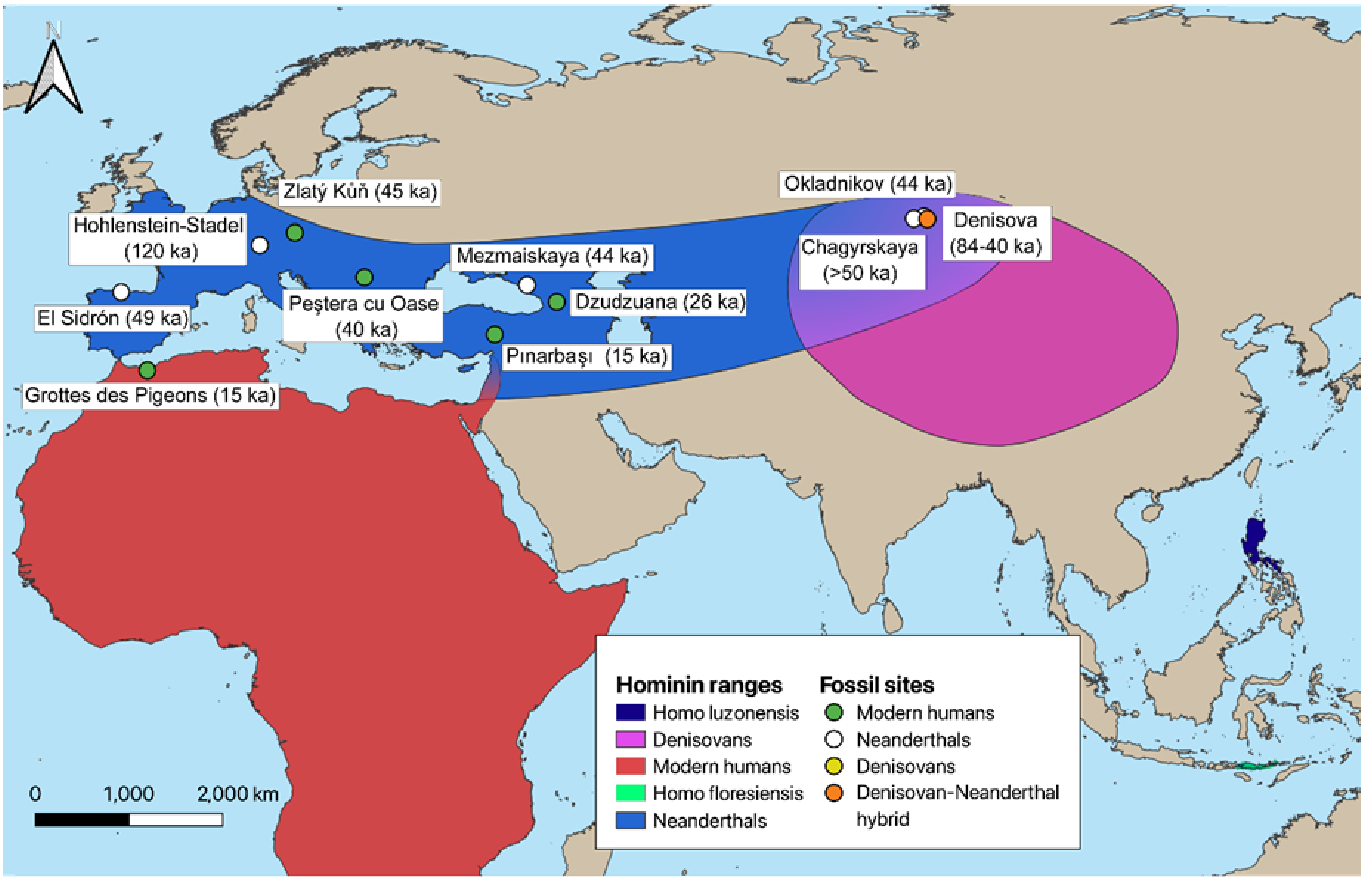


Figure 2: Global distribution of hominin species in the Late Pleistocene with key aDNA fossils mentioned in the article. Note that Denisova Cave contains both Neanderthals, Denisovans, and Neanderthal-Denisovan hybrid genomes. Note also the regions of overlap between Denisovans and Neanderthals in Siberia and modern humans and Neanderthals in the Levant. These regions likely served as areas of hybridisation due to gene exchange. Map by author in QGIS 3.30.2 and Inkscape 1.3. See Shea 2008; Higham *et al.* 2014; Fu *et al.* 2015; Kuhlwilm *et al.* 2016; Sutikna *et al.* 2016; Posth *et al.* 2017; Lazaridis *et al.* 2018; van de Loosdrecht *et al.* 2018; Détroit *et al.* 2019; Feldman *et al.* 2019; Dennell 2020; Petr *et al.* 2020; Hershkovitz *et al.* 2021; Skov *et al.* 2022; Slimak *et al*. 2022; 2023; Stringer and Crété 2022; Quilodrán *et al.* 2023; Peyrégne *et al.* 2024.

Groucutt *et al*. 2021). Meanwhile, Neanderthals (~440-40 ka), Denisovans (no official taxon; ~440-50 ka), *Homo floresiensis* (~700-50 ka), and *Homo luzonensis* (at least 60-50 ka) lived across Eurasia until 40-50 ka ago, see fig. 2 (Higham *et al.* 2014; Sutikna *et al.* 2016; Détroit *et al.* 2019; Slimak *et al.* 2022; 2023; Quilodrán *et al.* 2023; Peyrégne *et al.* 2024). At some point during the dispersals out of Africa , modern humans met and interacted with at least some of these hominins, evidenced by the ~2 % of Neanderthal DNA in modern non-African genomes (Green *et al.* 2010; Prüfer *et al.* 2014; Bergström *et al.* 2020; but see also Lohse and Frantz 2014) and ~2-4 % Denisovan DNA in genomes from East Asian and Australasian populations (Green *et al.* 2010; Bergström *et al.* 2020; Peyrégne *et al.* 2024). The most likely explanation for the genetic fingerprint of these ancient hominins in modern human populations is admixture, although the number, timing, and precise location of events is unclear (Sankararaman *et al.* 2012). Since all non-African populations share Neanderthal DNA, the admixture event is likely to have happened first in Southwest Asia, the necessary staging point for any migration out of Africa (Green *et al.* 2010).

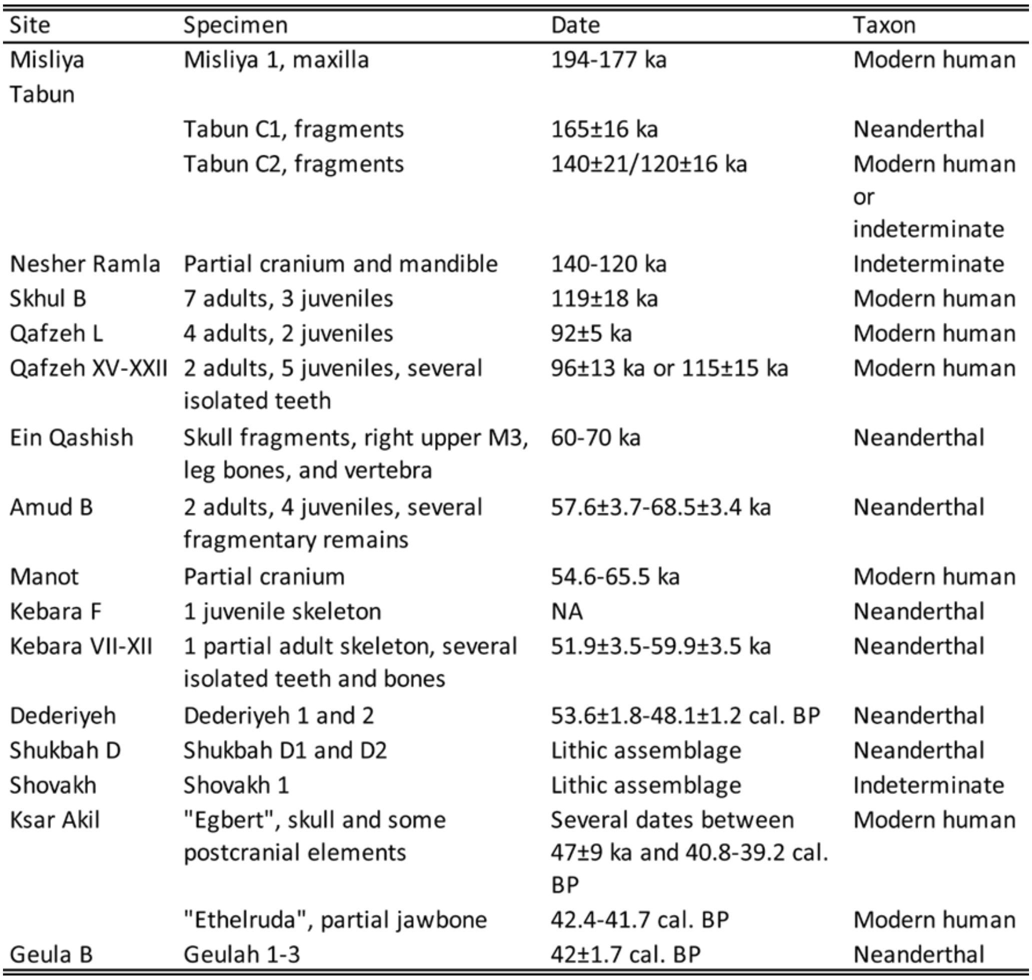
The early dispersals out of Africa have often been interpreted as “failed” attempts since they left no lasting genetic signature in contemporary human populations and were outcompeted by other hominin species (Rabett 2018). However, mounting evidence of early genetic admixture between Neanderthals and modern humans suggests that these dispersals were more dynamic. One study by Petr *et al.* (2020) sequenced parts of the Neanderthal Y chromosome, which is inherited solely through the paternal lineage. Their results showed that the Neanderthal Y chromosome was more closely related to modern humans than to Denisovans (Petr *et al.* 2020), despite modern humans splitting from Neanderthals and Denisovans ~550 ka ago, whereas Neanderthals only split from Denisovans ~400 ka, based on genetic estimates (Liu *et al.* 2021). It is worth noting that genetic estimates do not always overlap with the fossil evidence and might therefore not fully reflect the timing of speciation events (see Gómez-Robles 2019), but the degree of relative relatedness between lineages estimated genetically still stands. The close affinity between Neanderthal and modern human Y chromosomes can be explained by an admixture event of modern human DNA into Neanderthals around 370-100 ka ago (Petr *et al.* 2020). An earlier study showed that the lower boundary for modern human mitochondrial (mt) gene flow into Neanderthals was 270 ka ago, based on the mt genome of the Hohlenstein-Stadel Neanderthal femur from Germany (Posth *et al.* 2017). The nuclear genome of a Neanderthal from Denisova Cave in the Altai Mountains, Siberia moreover showed introgression from modern humans dated to ~100 ka ago (Kuhlwilm *et al.* 2016). However, this is not the case for all Neanderthals, which suggests that several biologically distinct populations existed throughout Eurasia. Some of these populations derived their genetic ancestry from admixture with modern humans moving into Southwest Asia from Africa during the past

300 ka. As soon as modern humans left Africa, then, they began interacting with other hominins and exchanging parts of their genomes.

In line with this evidence, Garcea (2012) has proposed two dispersals into Southwest Asia, one at 100 ka ago (OoA 2a) and a later dispersal at 50 ka ago (OoA 2b). Based on the genetic evidence cited above, but in contrast to Garcea (2012), OoA 2a does not reflect a single dispersal, but rather several earlier migrations that began as early as 300 ka ago. These dispersals left some genetic signatures in Neanderthal populations, but not in modern human populations. Determining whether the extinctions of these early human populations were the product of Neanderthal replacement, climate change, or something else requires further study. However, during OoA 2b, the opposite happened: every hominin species except our own ultimately went extinct. A key question in palaeoanthropology is determining why this happened (Rabett 2018).

Coexistence or conflict? Insights into social organisation and the interactions between Neanderthals and modern humans

The comprehensive fossil record of modern humans and Neanderthals in Southwest Asia, beginning with the Misliya and Tabun cave sites, situates the region as a key region for understanding the interactions between these hominins (Tab. 1; Fig.



Site	Specimen	Date	Taxon
Misliya	Misliya 1, maxilla	194-177 ka	Modern human
Tabun			
	Tabun C1, fragments	165±16 ka	Neanderthal
	Tabun C2, fragments	140±21/120±16 ka	Modern human or indeterminate
Nesher Ramla	Partial cranium and mandible	140-120 ka	Indeterminate
Skhul B	7 adults, 3 juveniles	119±18 ka	Modern human
Qafzeh L	4 adults, 2 juveniles	92±5 ka	Modern human
Qafzeh XV-XXII	2 adults, 5 juveniles, several isolated teeth	96±13 ka or 115±15 ka	Modern human
Ein Qashish	Skull fragments, right upper M3, leg bones, and vertebra	60-70 ka	Neanderthal
Amud B	2 adults, 4 juveniles, several fragmentary remains	57.6±3.7-68.5±3.4 ka	Neanderthal
Manot	Partial cranium	54.6-65.5 ka	Modern human
Kebara F	1 juvenile skeleton	NA	Neanderthal
Kebara VII-XII	1 partial adult skeleton, several isolated teeth and bones	51.9±3.5-59.9±3.5 ka	Neanderthal
Dederiyeh	Dederiyeh 1 and 2	53.6±1.8-48.1±1.2 cal. BP	Neanderthal
Shukbah D	Shukbah D1 and D2	Lithic assemblage	Neanderthal
Shovakh	Shovakh 1	Lithic assemblage	Indeterminate
Ksar Akil	"Egbert", skull and some postcranial elements	Several dates between 47±9 ka and 40.8-39.2 cal. BP	Modern human
	"Ethelruda", partial jawbone	42.4-41.7 cal. BP	Modern human
Geula B	Geulah 1-3	42±1.7 cal. BP	Neanderthal

Table 1: Hominin fossils from the Levant contemporary with OoA 2. Based on data from Shea (2008), Dennell (2020), Hershkovitz *et al.* (2021), and Stringer and Crété (2022).

3). Earlier studies based solely on archaeological and fossil evidence suggested that competition for limited resources led to continuous replacement of hominin groups in the Levant (Shea 2001; 2003; 2008) and across Eurasia (Stringer 2002; Scarre 2009). The palaeogenomic evidence shows that these hominins interbred, and an alternative view would be peaceful coexistence, at least occasionally. Lithic evidence from the Levant has also been interpreted in a similar manner with the appearance of "symbiotic industries" with both modern human and Neanderthal

Figure 3: Map of key Levantine fossil sites. Note the overlap between Neanderthals and modern humans. Most of the sites are high-altitude caves, making them higher-potential sites for Pleistocene aDNA recovery in the Levant, although the adverse effects that temperature plays on DNA preservation remains an issue. Map by author in QGIS 3.30.2 and Inkscape 1.3.

features (Bar-Yosef 2013). The continuous cohabitation of these hominins in the Levant means that the region is central to determine why OoA 2b eventually led to Neanderthal extinction and, by inference, the extinction of other hominins in other regions. Stewart and Stringer (2012) have proposed that an expanding modern human population concurrently with a contracting Neanderthal one (due to climatic stress) during OoA 2b would serve as an explanation, but this is difficult to identify indisputably in the archaeological record.

Palaeogenomics does provide evidence of modern human population expansion, however, specifically through negative selection against Neanderthal genes. The genome of a modern human from Peştera cu Oase in Romania, dated to 42-37 ka old, had 6-9 % Neanderthal DNA in his genome due to admixture 4-6 generations back (Fu *et al.* 2015). This is higher than what is found in modern humans today, and other genomes closer to admixture also show greater amounts of Neanderthal DNA in larger regions of the genome (Fu *et al.* 2014; 2016; Prüfer *et al.* 2021). In modern populations, inherited Neanderthal DNA is found in certain genes (e.g., BNC2 and OCA2) which have been linked to freckling and lighter skin, hair, and eye pigmentation in Eurasian populations, possibly providing adaptive benefits to novel environments (Gittelman *et al.* 2016; Dannemann and Racimo 2018; Williams 2019; McArthur *et al.* 2021; Koller *et al.* 2022; Reilly *et al.* 2022). There is moreover an overlap in those parts of the genome that have no trace of an admixture event with Neanderthals in both modern and prehistoric populations close to admixture (Hajdinjak *et al.* 2021), which suggests that selection worked rapidly against most Neanderthal genes inherited by immediate offspring. This might have only left those genes which provided beneficial adaptations for modern human populations.

There are two mechanisms that could have produced the distinct genomic signature of Neanderthal DNA seen in modern populations: first, larger modern human than Neanderthal populations could have led to pruning selection of introgressed genes, leaving only those which led to increased fitness, or, second, semi-sterile offspring resulting from hybridisation (Dannemann and Racimo 2018). Although the latter has been favoured by some researchers (e.g., Dannemann and Racimo 2018; Williams 2019), the genetic evidence in conjunction with fossil and archaeological data suggests a process whereby Neanderthal females were incorporated into modern human groups, which would have depleted the Neanderthal gene pool (Stringer and Crété 2022). This is based genetically on the size of modern human compared to Neanderthal forager bands as evidenced by runs of homozygosity (ROH), and genetic evidence of patrilocality amongst Neanderthals. ROH are contiguous segments of the genome that are present in individuals due to parents transmitting identical haplotypes in their offspring. Long ROHs in an individual imply that their parents shared a recent common ancestor, which can provide insights into social organisation and population size, as this could be due to either a small available gene pool or cultural preferences (Ceballos *et al.* 2018). Neanderthal genomes consistently show longer ROH than those of ancient modern humans (Prüfer *et al.* 2014; 2017; Skov *et al.* 2022; Slimak *et al.* 2023), indicating that they probably had smaller populations. Genetically inferred population estimates based on ROH suggest groups of up to 20 individuals (Skov *et al.* 2022), consistent with archaeological estimates of Neanderthal population sizes around 12-24 individuals (Hayden 2012). This is supported by ethnographic evidence with a mean size of forager bands of 28-30 individuals in modern groups across the world (Bird *et al.* 2019, table 1). The palaeogenomic evidence thus suggests larger modern human forager bands than Neanderthal ones.

The second point is inferred through studies of mtDNA (inherited solely through the maternal line). A study by Lalueza-Fox *et al.* (2011) of Neanderthals from El Sidrón Cave in Spain showed that females carried different mt haplotypes, suggesting patrilocal mating behaviour. A more recent study published genome-wide nuclear data, as well as Y-chromosomal and mtDNA, of a group of closely related Neanderthals from southern Siberia (Skov *et al.* 2022). It showed significantly lower Y-chromosomal than mtDNA diversity in the group, which was best explained by patrilocal mating behaviour since Y chromosomes are solely inherited through the paternal line (Skov *et al.* 2022). Although the data is still sparse, it does suggest that Neanderthals practised patrilocality across their range of habitation. If future studies corroborate this data, explanations of Neanderthal extinction would need to factor in processes through which Neanderthal females either voluntarily or coercively chose modern human mating companions rather than Neanderthal ones. This would create a process by which females were absorbed into modern human groups, depleting the gene pool of Neanderthals.

Although admixture would have been common, as evidenced by admixture in several independent modern human genetic lineages, including some that went extinct (Fu *et al.* 2014; 2015; Prüfer *et al.* 2021), as well as the discovery of a hominin hybrid in the fossil record (Slon *et al.* 2018), it was not always the rule (Hajdinjak *et al.* 2018). A Southwest Asian Palaeolithic population of modern humans, which is yet to be sampled directly but evident from Neolithic genomes from across Eurasia, had little to no Neanderthal DNA (Lazaridis *et al.* 2014; 2016; 2018). Although conclusions about the genetic history of this unsampled population should await direct sequencing of individuals belonging to it, their higher affinity with ancient Southwest Asian populations suggests that it likely lived somewhere in the region. This would have made it geographically close to concurrent Neanderthal populations, highlighting the fact that while some populations of modern humans and Neanderthals interbred, others did not. Interestingly, recent modelling work has shown that Neanderthal ancestry was diluted in European populations following the spread of Neolithic farmers from Southwest Asia (Quilodrán *et al.* 2023), with the presence of a basal Eurasian population without Neanderthal introgression in Southwest Asia admixing with other Southwest Asian populations a possible explanation for the relative lower levels of Neanderthal ancestry in the region. Nevertheless, fully understanding the causes behind this variability requires further work, but Southwest Asia, with its long occupational history of both modern humans and Neanderthals, is ideally suited to test these hypotheses.

The most significant shortcoming of the palaeogenomic evidence is the low geographic coverage. It has been suggested that Neanderthals exhibited high variation in social organisation analogous to modern humans (Zilhão 2014), and genomic data from a wider geographic area is therefore needed to better understand Neanderthal social organisation and their genetic relation to modern humans. Southwest Asia is particularly well suited to produce such data, as it can be interpreted in conjunction with the otherwise rich archaeological and fossil record.

The formation of Southwest Asian ancestries

The oldest sequenced genomes directly from Southwest Asia are 26 ka old and belong to two individuals from Dzudzuana Cave, Georgia (Lazaridis *et al.* 2018), although the publication remains in preprint. Nevertheless, the genomes highlight the current dearth of genetic understanding of the Southwest Asian Palaeolithic until rather late in the Upper Palaeolithic. Based on evidence from Late Upper Palaeolithic and Neolithic genomes derived from Georgia, Iran, and Anatolia, it was proposed that the population structure of the region formed shortly after OoA 2b (the second migration of modern humans out of Africa 50 ka ago, see above) and continued throughout the Upper Palaeolithic (Jones *et al.* 2015; Gallego-Llorente *et al.* 2016; Feldman *et al.* 2019). However, the Dzudzuana individuals were closer related to early Neolithic farmers from Anatolia than Late Upper Palaeolithic foragers from the Caucasus, suggesting that the population structure of the Caucasus formed within the last 20 ka, after the Last Glacial Maximum (LGM) (Lazaridis *et al.* 2018). This is also the case in North Africa, where Later Stone Age individuals dated to 15 ka ago from Morocco have up to 63.5 % Natufian ancestry (~15-11 ka), providing good evidence of Epipalaeolithic migrations from the Levant into North Africa (van de Loosdrecht *et al.* 2018). These migrations had already been supported earlier on the evidence that a particular mitochondrial haplogroup, U6, is most commonly found in modern populations in Northwestern Africa despite forming in Southeastern Europe 35 ka ago (Hervella *et al.* 2016). In addition, autochthonous North African ancestry decreases gradually in populations closer to the Levant while Southwest Asian ancestry increases, likely owing to migrations more than 12 ka ago (Henn *et al.* 2012). These migrations were continuous, evidenced by the fact that early Neolithic farmers from Morocco traced part of their ancestry to Natufian introgression 11 ka ago and Pre-Pottery Neolithic (~12-8.5 ka) farmers from the Levant 8.5 ka ago (Fregel *et al.* 2018). These migrations are not only attested genetically but are also evident from lithic evidence (Garcea 2016).

The mounting evidence of consistent migrations between Africa and the Levant have forced researchers to change previous assumptions about Neanderthal introgression in modern humans. Earlier models showed clear traces of hominin admixture in African populations (Sánchez-Quinto *et al.* 2012; Hsieh *et al.* 2016; Lorente-Galdos *et al.* 2019) and this was recently partly quantified as low amounts of Neanderthal introgression in African populations deriving from Eurasian return migrations during the Upper Palaeolithic and later (Chen *et al.* 2020). Significantly, this has influenced previous models used to quantify Neanderthal introgression in non-Africans, showing that East Asians do not possess 20 % more Neanderthal DNA than West Europeans, as previously proposed (Nielsen *et al.* 2017), but only 8 % (Chen *et al.* 2020). Thus, previous models showing that admixture needed to happen continuously to produce modern population structure need to be revised (Villanea and Schraiber 2019).

This should not lead to the conclusion that Upper Palaeolithic migration and biological exchange were on par with those seen in the later agricultural societies of the region (Orlando 2020). Indeed, the bulk of studies continuously support a scenario wherein Upper Palaeolithic population structures were largely continuous due to isolation or lack of interaction between distinct groups, and thus that Neolithic populations derived locally rather than due to external migrations (Jones *et al.* 2015; Broushaki *et al.* 2016; Gallego-Llorente *et al.* 2016; Lazaridis *et al.* 2016; Feldman *et al.* 2019). Nevertheless, Europe, which is much better studied, is beginning to showcase a more dynamic and varied history of genetic interaction between forager groups even predating the LGM (see Posth *et al.* 2023), and it is likely that future publication of genomes from varied places within Southwest Asia will significantly inform our understanding of this period in the region. For example, the palaeogenomic resolution in Southwest Asia is still far too low to quantify the degree to which Upper Palaeolithic and Epipalaeolithic foragers exchanged genes compared to materials and ideas in local and regional interaction spheres (Hill *et al.* 2011; Richter *et al.* 2011; Bird *et al.* 2019; Singh and Glowacki 2022). More, and especially older, genomes from the region would significantly help to shed light on the biological history of foragers in Southwest Asia, from the appearance of the earliest modern humans to the advent of agriculture.

Filling out the DNA dearth

Despite the importance of Southwest Asia for understanding the pre-agricultural history of our species, there is a significant lack of genomes from this region compared to Europe (Mallick and Reich 2023; Mallick *et al.* 2023). Although this is partly due to research bias (Gokcumen and Frachetti 2020; Tsosie *et al.* 2021), a major limitation for the sampling of Southwest Asian genomes is poorly preserved aDNA. The high temperatures of the region impact preservation adversely compared to regions farther away from the equator (Smith *et al.* 2003; Allentoft *et al.* 2012; Hagelberg *et al.* 2015). In addition, the increasing scarcity of fossils when moving further back in time complicates the sequencing of Palaeolithic genomes, not least in Southwest Asia, as the fossils themselves become increasingly more valuable

(Olalde and Posth 2020). Consequently, Palaeolithic genetic data from the region is currently very sparse and it is necessary to draw significantly on external genomes and extrapolate the findings to Southwest Asia.

One possible alternative to direct DNA sequencing from fossils is the growing field of environmental DNA (eDNA). This allows for extraction of DNA preserved in sediments, ice, or water (Pedersen *et al* 2015), with several studies having now managed to identify DNA from rare taxa such as hominins at sites (Gelabert *et al.* 2021; Massilani *et al.* 2021; Vernot *et al.* 2021; Slon *et al.* 2017; Zavala *et al.* 2021; Zhang *et al.* 2020). Despite past arguments about possible movement of DNA through layers (*e.g.*, Haile *et al.* 2007), the combination of microstratigraphy with eDNA sequencing has shown that the DNA can remain highly localised in fragments of bones and coprolites in sediments, allowing for a precise linking of the sequenced eDNA to the stratigraphic record of a site (Massilani *et al.* 2021). Although Pleistocene eDNA has been recovered from El Sidrón Cave in Spain and Satsurblia Cave in Georgia (Vernot *et al.* 2021; Slon *et al.* 2017), attempts to recover eDNA dating to this period from warmer regions, including Kebara Cave in Israel, have been unsuccessful (Massilani *et al.* 2021). The adverse effects of high temperatures on DNA preservation thus remains a major issue, and can likely only be solved by novel techniques capable of sequencing even more miniscule amounts of DNA than is currently possible. Until this is achieved, the focus should be on retrieving DNA from colder parts of the region (whether sequenced from sediments or fossils), with higher-altitude sites in the Pontic and Caucasus Mountains providing the most promising candidates due to their comparably lower mean temperatures (Fig. 4).

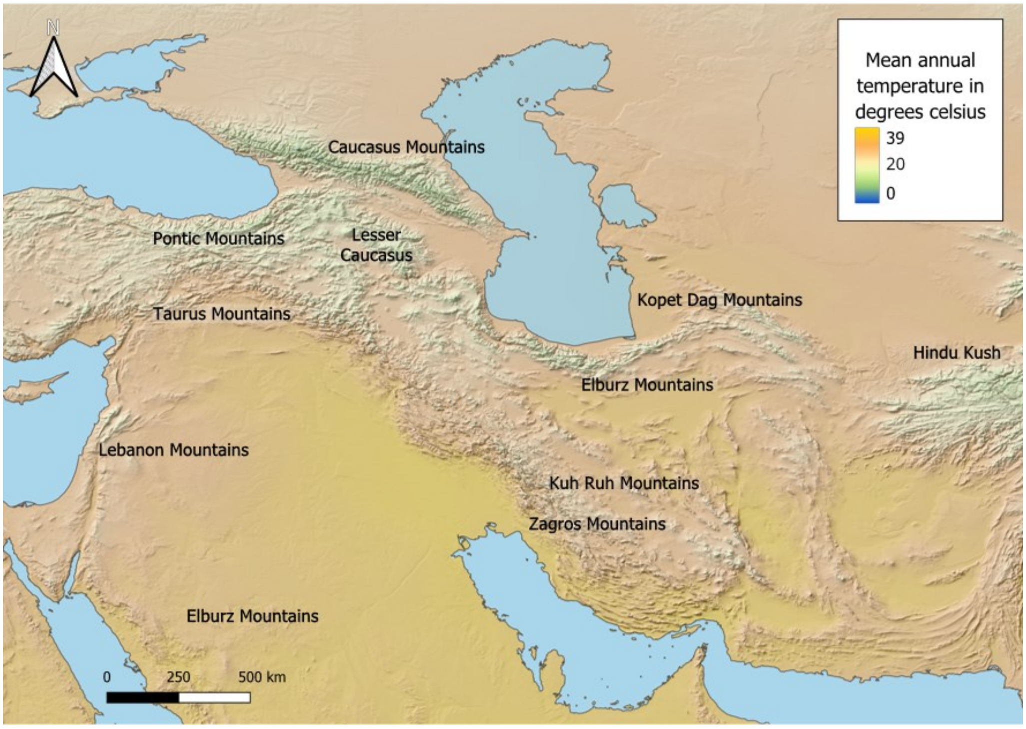


Figure 4: Mean annual August temperatures across Southwest Asia from 1979-2013. Note the lower temperatures in especially the Caucasus and Pontic Mountains, indicating they might be high potential regions for aDNA recovery in the region. Data from Karger *et al.* (2017; 2018)- Map by author in QGIS 3.30.2.

To further ensure finer genetic resolution for the Southwest Asian Palaeolithic, it is moreover imperative that research groups report negative research findings systematically to create an environment of equal collaboration and novel datasets that can be used to better understand DNA preservation and degradation in the region and beyond (Alpaslan-Roodenberg *et al.* 2021). If combined with a focus on local capacity building and greater integration of stakeholder communities and individuals throughout the research process (see Ávila-Arcos *et al.* 2023), it might be possible to move beyond the younger genomes that currently predominate the field in Southwest Asia (see Fig. 1) and instead focus on providing a better resolution of the currently sparse Palaeolithic record. This importantly requires greater involvement of archaeological viewpoints throughout the design and application of studies to counter issues leveraged by the archaeological community against palaeogenomic studies, e.g., an oversimplification of complex phenomena such as migrations (Roberts and Vander Linden 2011; Heyd 2017; Furholt 2018). This extends to the Palaeolithic, where debates such as whether the Initial Upper Palaeolithic derived from migrations or local developments (see Kuhn 2003; Meignen 2012; Olszewski 2017; Greenbaum *et al.* 2019; Goring-Morris and Belfer-Cohen 2020; Boaretto *et al.* 2021) could be helpfully illuminated by genetic data, if theoretical insights from archaeology are used to interpret the palaeogenomic results. This would provide a starting point for the formulation of common theoretical and analytical frameworks, which are necessary for the findings of palaeogenomics to remain important to archaeologists and anthropologists. It would also ensure that the tendency for genetic data to take unsubstantiated precedence over archaeological, morphological, and ethnographic evidence (Horsburgh 2015; Jones and Bösl 2021) would be less prevalent. If these issues are resolved, palaeogenomics is likely to revolutionise our understanding of the Palaeolithic in Southwest Asia just as it has in Europe.

Conclusions

Palaeogenomics has significantly impacted our interpretations of human prehistory by adding a novel set of data, and in this review, it has been highlighted how the field has begun to transform our interpretations of the Southwest Asian Palaeolithic. It has shown that admixture in the region during Out of Africa 2b led to novel adaptations which likely made modern humans more fit in non-African environments, and that the depletion of the Neanderthal gene pool was facilitated by the interactions between modern humans and Neanderthals. However, the nature of these interactions was highly complex and, although admixture occurred continuously, it was not always the rule. Moreover, movement between the Levant and North Africa throughout the Upper Palaeolithic now make it evident that the population structures of these regions formed after the Last Glacial Maximum. But poor DNA preservation and the lack of a sustained research focus has resulted in a relatively poor resolution of this key period in the prehistory of Southwest Asia. Stronger integration between archaeology and palaeogenomics, along with attempts to better sequence the poorly preserved DNA of the region through strategic targeting of high potential sites for DNA preservation, can help solve this issue and move genetic research of extinct hominins and early forager groups into a new era. If this can be done, aDNA has the potential to provide many new insights into the deep prehistory of Southwest Asia.

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Dataset
Dataset available as Suppl. Dataset 1 at tidsskrift.dk/chronolog.