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WHAT'S NEW IN CENTRAL ASIA?

After Dubois' discovery of the Trinil fossils, the "Out of Asia" theory was the dominant hypothesis on human evolution for almost 50 years. Some proponents, such as Roy Chapman Andrews (the real life model for Indiana Jones!) and Henry Fairfield Osborne placed the origin of modern humans in Central Asia, which led them to start the first modern and interdisciplinary expedition, "The Central Asiatic Expedition", lasting over a decade. They did not find any human remains, but were the first to discover dinosaur nests and the very rich palaeontological sites of Xinjiang and the Gobi (Gallenkamp, 2002).

After this, interest in this region strongly declined, largely because new discoveries in Africa and the Near East captured the interest of the palaeoanthropological community. However, scholars in the Soviet Union continued intensive research in Central Asia (e.g. Movius, 1953; Ranov and Davis, 1979; Davis and Ranov, 1999).

However, it is only through the efforts of Anatoly Derevianko and his collaborators that Central Asia (in a geographically broad sense), and especially the Altai region, is now beginning to get its deserved place in the spotlight of human evolution. This has been achieved not only though the excavations and other scientific work of Anatoly Derevianko. More than anybody else he has also furthered the scientific communication between Central Asian scholars and the rest of the world, by setting an example of openness in organizing conferences and inviting colleagues to see the material first hand. In his work in the Altai region he has also been a pioneer in the application of new methods in archaeology. Here, we will first summarize the new hominin finds in Central Asia, and then discuss some major questions they raise.

Denisova Cave. Denisova Cave preserves a long cultural and geological sequence that covers a large part of the late Pleistocene (Derevianko et al., 2003). This makes it the reference sequence for the Altai to which all other sites can be compared. Layers 22–12 contain a middle Paleolithic industry, Layer 11 is one of the few initial Upper Paleolithic assemblages in the region, Layers 10 and 9 contain later UP industries, while Layers 8 and above are from the Holocene. Layer 22.1, at the bottom of the sequence delivered a very worn hominid lower second deciduous molar, which is undiagnostic, but it is the oldest known hominin fossil from Central Asia, deriving from OIS 7 or OIS 5 (200–120 ka BP).

The hominid remains from Layer 11 are more numerous. A fragment of a distal phalanx of a child (Layer 11.2, Eastern Gallery) is morphologically not diagnostic, but preserves large amounts of DNA. This allowed not only the study of the mtDNA (Krause et al., 2010) but also of the nuclear DNA (Reich et al., 2010) and most recently the generation of the first high coverage genome of a fossil human (Meyer et al., 2012). This specimen was the first evidence for the existence of a hitherto unknown group of hominids. This group was designated "Denisovans" (Reich et al., 2010) in analogy to the "Neandertals", who were first described from the Neander Valley in Germany. Analyses of the nuclear DNA show that Denisovans interbred with the ancestors of present day Melanesians, resulting in a Denisovan contribution of about 3–6 % in recent Papuans and Australian aborigines. The geographic distribution of Denisovan ancestry has been used to argue that Denisovans were present in Southeast Asia (Reich et al., 2011). Although it is not known if they were both in the Altai and in Southeast Asia at the same time, they are likely to have been present over a wide geographic range at least at some points in their history.

Several other hominin bone fragments have been found in the Eastern Gallery, among them a proximal pedal phalanx in Layer 11.4 (Mednikova, 2011). Surprisingly, this specimen is not a Denisovan, but based both on its mitochondrial and nuclear genome a Neanderthal. This shows that the cave was successively occupied by Neanderthals and Denisovans, as well as later on by modern humans.

Two other specimens from Denisova Cave allow the study the dental morphology of Denisovans. A very large upper molar from Layer 11.1 in the South Gallery shows robust splaying roots and a bulging crown, rather unlike the morphology seen in Neanderthals, and more comparable to Middle Pleistocene *Homo*. This specimen carries a mtDNA lineage that is closely related to the child phalanx (Reich et al., 2010).

In the course of the 2010 excavation, a large tooth fragment was found at the boundary of Layer 11.4 and Layer 12. Based on its nuclear and mitochondrial DNA, this specimen is a Denisovan, . It is a very large and anomalous upper M3, low crowned with five cusps. Both teeth are far outside the size range seen in Neandertals, *Homo erectus* and later Pleistocene hominids.

Okladnikov Cave. The second important site with fossil hominins in the Altai, Okladnikov cave, was excavated in the mid-1980s by S. Markin and A.P. Derevianko. The site contained a rich lithic industry of Mousterian affinities, originally called the Altai Mousterian (Derevianko and Markin, 1992), and more recently the Sibiryachikha culture (Derevianko and Markin, 2011). The hominin remains consist of five teeth and nine postcranial fragments, which derive from at least four individuals. Morphologically, the material shares some plesiomorphic traits with Neanderthals, but especially the dentition lacks the typical autapomorphies seen in Neandertals such as the mid-trigonid crest of the lower molars (Viola, 2009; Viola et al., 2011). The postcranial material is similar to Neandertals, but is characterized by its gracility.

In collaboration with Anatoly Derevianko, Krause and collaborators (2007) presented mtDNA sequences from two fragments from Okladnikov cave, a juvenile humerus diaphysis and a femur fragment probably belonging to the same individual. The mtDNA sequences of the HVR I (hypervariable region I) fall into the Neandertal clade. This was the first evidence for the presence of Neandertals east of Uzbekistan.

Obi-Rakhmat. The site of Obi-Rakhmat was known since the 1960s (Suleimanov, 1972). Scientific excavations were restarted in 1997 by A.P. Derevianko and A.I. Krivoshapkin. The site contains an about 8 m thick stratigraphic sequence rich in lithics and faunal remains. The industry has been interpreted either as an MP/UP transitional industry (Krivoshapkin et al., 2006) or as a blade based Middle Palaeolithic similar to blade rich MP industries in the Near East (Meignen, pers. comm.).

The hominin remains consist of about 150 fragments of a child cranium from Layer 16, including six teeth, the left parietal and both petrosals.

The dentition of Obi-Rakhmat 1 shows numerous characteristics that align it closely with the Neandertals (Glantz et al., 2008; Bailey et al., 2008). The strong shoveling of the I^2 and C^{sup} and the rhomboid shape of the M^1 are probably the most diagnostic, even though it is impossible to assess the degree of labial convexity in the I^2. The high frequency of these traits is derived in Neandertals (Bailey, 2002). The presence of slight taurodontism in the M^1, as well as the large size of all teeth are plesiomorphic traits seen in Neandertals, but also in other non-modern humans. The bony labyrinth shows an inferiorly placed posterior semicircular canal, a trait autapomorphic in Neandertals (Hublin et al., 1996; Spoor et al., 2003).

Interestingly, the cranial remains show a somewhat different picture. The parietal of Obi-Rakhmat 1 is remarkably long, well outside the range of variation of both juvenile and adult Neandertals, while it is rather similar to Early and Upper Palaeolithic modern humans. Similarly, the fragments of the temporal lack the apomorphies seen in Neandertals, such as a highly placed external acoustic meatus and marked suprameatal and supramastoid crests. This fact can not be explained by the age of OR-1, as at least the high position of the external acoustic meatus is visible in much younger Neandertal children (Glantz et al., 2008).

This mosaic morphology of derived Neandertal traits in the dentition and bony labyrinth, and derived modern human features in the cranial bones is hard to interpret. However, it shows how hard it is to apply morphological categories defined in Europe and the Near East to Central Asia.

These discoveries pose several questions of both a technical and general nature that are of great importance for the understanding of the origin of modern humans and their interactions with archaic humans. Below, we briefly outline a few of these questions.

Molecular preservation in Denisova Cave. The initial extraction of DNA and analysis of the mitochondrial DNA revealed two remarkable findings. Firstly, the absolute amount of DNA in the bone was very high, and, secondly, the percentage of endogenous DNA was between 60 and 70 percent, while the percentage of bacterial DNA was only around 30 to 40 percent (Reich et al., 2010). This is very unusual. Typically, when Late Pleistocene remains are studied, less than one percent of the DNA extracted is endogenous to the bone, while the waste majority is made up of DNA from microbes that have colonized the bone after its deposition. The only systematic exception to this is the permafrost where for example mammoth remains can contain similar relative amounts of endogenous DNA (e.g. Poinar et al., 2006).

Currently, it is a mystery why DNA preservation in some specimens found in Denisova Cave is so exceptional. Interestingly, not all human remains in Denisova

Cave show excellent DNA preservation. The two molars show preservation much more typical of other sites, with less than 0.3 % of the DNA being endogenous to the fossil. In contrast, the pedal phalanx found in Layer 11.4 shows preservation similar to the distal phalanx from Layer 11.2 In the future, it would be very interesting to analyze the detailed physical conditions surrounding bones found in Denisova Cave and try to correlate this with DNA preservation. Perhaps this would allow a deeper understanding of why DNA can sometimes be preserved over long time periods and why sometimes microbial growth is limited. This would be very useful for a more directed search for DNA at this as well as other sites in the future.

The excellent DNA preservation in Denisova Cave has allowed unprecedented genetic insights into human prehistory. In combination with new sensitive methods for DNA retrieval and preparation for sequencing, less than 30 mg of bone from the finger phalanx has allowed a complete genome sequence of a quality similar to that can be determined from humans living today to be determined (Meyer et al., 2012). Similarly, the foot phalanx has allowed a Neandertal genome of similar quality to be determined (Pruefer et al., unpublished). Thus, Denisova Cave has yielded the reference genomes to which all other future genome sequences from these groups of humans will be compared. Denisova Cave is thus destined to be of pivotal importance for future genetic work on the origin and history of archaic humans.

Neanderthal geographic range and variability. Teshik-Tash has traditionally been assumed to be at the eastern limit of Neanderthal distribution, but the new finds from Denisova and Okladnikov caves show unambiguously that their actual range was significantly larger. Does this mean that the Neandertals could have ranged even further to the east? Answering this question is complicated by the dearth of evidence, as there are no Middle Palaeolithic associated human remains in Eastern Siberia. Unfortunately, the Salkhit cranium from Mongolia, described by Coppens and colleagues (2008) as showing Neandertal characteristics, is most likely a late Upper Palaeolithic modern human (N. Teyssandier, pers. comm., B.V.'s own observations). Hopefully, future work in Siberia as well as in China and elsewhere will allow this question to be addressed.

The related question is whether by only focusing on the European Neanderthals scientists have underestimated morphological variability of Neandertals. It has been observed that there is geographic variation in the morphology of Neandertals (e.g. McCown and Keith, 1939; Endo and Kimura, 1970; Vandermeersch, 1981, 1989; Condemi, 1988; Voisin, 2007). One of the problems is that for most purposes, the „typical" Neandertal is still considered to be represented by one of the well preserved skeletons from France, such as La Ferrassie 1 or La Chapelle aux Saints 1, even though these specimens are just one extreme of a geographic and morphological continuum stretching from Western Europe to the Near East and Central Asia. The differences between Neandertals from Western Europe and the Near East are numerous, and found in most anatomical regions (for a detailed list of characters see Voisin, 2007), for example stature (Vandermeersch, 1981; Endo and Kimura, 1970), body proportions (Churchill, 1998) and height of the cranial vault (Condemi, 1992). The last is of particular interest, as one of the arguments Weidenreich used to refute the assignment of Teshik-Tash 1 to the Neandertals is the great cranial height of the specimen. We now know that this trait is also present in Near Eastern Neandertals.

Several explanations for the morphological differences seen between the Western European and Near Eastern Neanderthals have been put forward. One approach is to completely deny the presence of Neandertals in the Near East, and to see a single evolving population that encompasses both the early anatomically modern humans (Qafzeh, Skhul) and "Near Eastern Neandertals" (e.g. McCown and Keith, 1939; Arensburg and Belfer-Cohen, 1998; Kramer, Grummett, Wolpoff, 2001).

Another one, originally proposed by Vandermeersch (1978), and later expanded on by Condemi (1988) is that the expansion of Neandertals from Europe to the Near East took place at a time when some of the typical traits were not yet fixed in the ancestral population, maybe around OIS 6 to 5e (190–120 ka BP). Geographic isolation after this would have hindered gene flow between the two populations, resulting in the differences between them. This hypothesis is supported by morphological similarities between early Neandertals such as Saccopastore 1 and 2, and the Near Eastern Neandertals. In addition, the limb proportions of Near Eastern Neandertals, despite being slightly different from the European Neandertals, still indicate a certain adaptation to colder climates, which could be taken as an indication that their ancestors came from a colder area (Condemi, 1988).

It has also been proposed (e.g. Trinkaus, 1983, 1984) that the Near Eastern Neanderthals are the result of a local evolution, starting with fossils such as the Zuttiyeh skull, and later resulting in the evolution of early anatomically modern humans. With the redating of the Skhul and Qafzeh fossils (Stringer et al., 1989; McDermott et al., 1993; Gruün et al., 1995), which are now older than most Neandertal remains from the region, this hypothesis seems to have been disproved.

An interesting new hypothesis was put forward by Voisin (2007), who sees a clear cline of Neanderthal morphology from the West to the East – with the Neandertal traits getting more and more diluted as one goes to the East. In his opinion, this fact can be best explained using a model of speciation by distance, as seen in ring species. Here, two extremes of a cline are connected by a succession of interbreeding groups, but interbreeding is not possible between the two ends of the distribution. The elegance of this hypothesis is that it explains the clinal variation in Neandertals as well as the absence (or scarcity) of hybridization in Western Europe.

In the future, genetic analyses may shed light on the geographic variation and population history of Neandertals. However, so far, almost all analyses have been based only on mtDNA which tend to yield a limited view of relationships, influenced by stochastic events. One analysis of Neandertal mtDNA by Fabre and colleagues (2009) has been taken to support the idea of distinct geographic groups. Using simulations, they compared different models of Neandertal genetic variability, and consider the presence of three geographic groups, one in Western Europe, one in the Mediterranean region and one in Central Asia as the most likely. Dalen et al. has suggested a late turnover of Neandertal populations in western Eurasia that would not have affected Central Asia (Dalen et al., 2012). However, recent analyses of mtDNA sequence from Denisova suggest that mtDNA closely related to those found in Western Europe existed also in the Altai (Sawyer et al., pers. comm.). We expect that analyses of nuclear DNA from the Altai, the Caucasus and Western Europe will eventually shed new light on the population history of Neandertals in both time and space.

Denisovan geographic range and variability. The study of DNA from the distal phalanx from Layer 11.2 has revealed that this Denisovan individual comes from a group of humans that share an origin with Neandertals, but subsequently had a long independent history separate from that of Neandertals. Presently, it is unknown how widespread Denisovans were in the past. However, comparisons of DNA sequences in present-day humans have revealed that Denisovans have contributed genetic material to present-day people living in Melanesia. Thus, it is likely that they have at some point during their history been present not only in the Altai Region but also in Southeast Asia. Future work will have to address when they were present where in Asia. This can either be achieved by future discoveries in Denisova Cave which might allow their morphology to be described. This would allow other finds elsewhere in Asia to be attributed to this group of humans. Alternatively, and not mutually exclusively, sites elsewhere in Asia might be investigated with respect to DNA preservation. This may result in that Denisovans, or groups closely related to them, might be found elsewhere in Asia.

Very little is known about variability among Denisovans, since only three remains of them, all from Denisova Cave, are presently known. However, while the mtDNA of the finger phalanx and the molar differ by only two nucleotide differences (Reich et al., 2010), the mtDNA of the second molar is substantially more divergent. Although the differences in absolute age between these three individuals are unclear, this shows that Denisovans harbored some extent of genetic variation. This is born out by an analysis of the two nuclear genomes, one derived from the mother and one from the father, carried by the finger phalanx individual. This shows that the extent of genetic diversity was smaller than that of modern humans who were contemporaneous with them. It also shows that their genetic diversity and thus their population size started to decrease at a point in time when modern humans started to expand in size. This shows that Denisovans had a population history very different from that of modern humans.

Interbreeding - a pervasive factor in human evolution. Two genomes of archaic humans have so far been sequenced. The Neandertal genome was initially sequenced from three bones from Vindija Cave in Croatia. These bones contained less than 4 % endogenous DNA and allowed a rough draft of the Neandertal genome to be established where about 55 % of all DNA sequences were represented (Green et al., 2010). The second genome is from the finger phalanx in Denisova cave and allowed about 70 % of all DNA sequences to be determined (Reich et al., 2010). More recently, the complete genome of the Denisova phalanx has been determined (Meyer et al., 2012) and the toe phalanx has recently allowed a Neandertal genome of high quality to be determined (Prüfer et al., unpublished). These genomes have radically changed the view of the genetic origins of modern human.

Analyses of the Neandertal genome showed that all present-day people outside Africa carry in the order of 2–5 % of Neandertal DNA, and people in eastern Eurasia and Native Americans carry about 20 % more Neandertal DNA than people in western Eurasia (Meyer et al., 2012). It has also been shown that the Neandertal contribution to present-day humans occurred in the order of 40,000 to 90,000 years ago (Sankararaman et al., 2012).

Analyses of the Denisova genome has furthermore shown that up to 5 % of the genome of people in Papua New Guinea, Aboriginal Australians and elsewhere in Melanesia come from Denisovans. Thus, the analysis of two archaic genomes has yielded evidence for at least two independent cases of mixture between ancestors of present-day humans and archaic human groups (Fig. 1). Although other explanations are possible (Meyer et al., 2012), it is furthermore possible that two different cases of mixture between modern humans and Neandertals occurred due to the higher amount Neandertal ancestry detected in eastern Eurasia than in western Eurasia.

Interestingly, the Denisova genome may hint at even another case of mixture between hominin groups. The Denisovan mtDNA differs from the nuclear genome in that it is not most closely related to the Neandertal mtDNA but diverges about one million years ago from the lineage leading to the common mtDNA ancestor of Neandertals and present-day

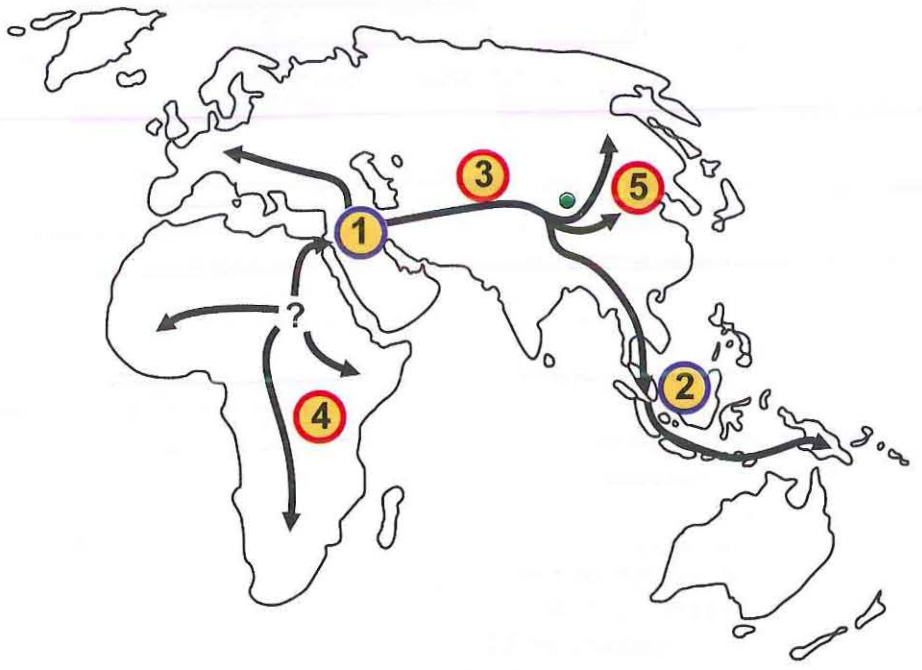

Fig. 1. A map showing putative cases of interbreeding among hominin groups.

1 – Admixture between modern humans and Neandertals resulted in that all present-day people outside Africa carry 1–5 % DNA derived from Neandertals. A possible location for this admixture is in the Middle East (Green et al., 2010).

2 – Denisovans has contributed in the order of 5 % of the DNA to present-day people in Melanesia. A possible location for this is Southeast Asia (Reich et al., 2010).

3 – Present-day people in eastern Asia carry about 20 % more Neandertal-derived DNA than people in Europe. It is possible that this is due to additional admixture between Neandertals and modern humans in Asia (although other explanations are also possible (Meyer et al., 2012).

4 – Patterns of genetic variation in present-day Africans suggest that extinct groups contributed to the genomes of present-day people in Africa (Hammer et al., 2011).

5 – Mitochondrial DNA sequences and other patterns in the genomes of Denisovans raise the possibility that they have interbred with another archaic group in Asia (although other explanations are also possible) (Reich et al., 2010). Blue circles indicate admixture events for which the evidence is strong, red circles those for which there are putative indications. A green dot indicates the approximate location of Denisova Cave.

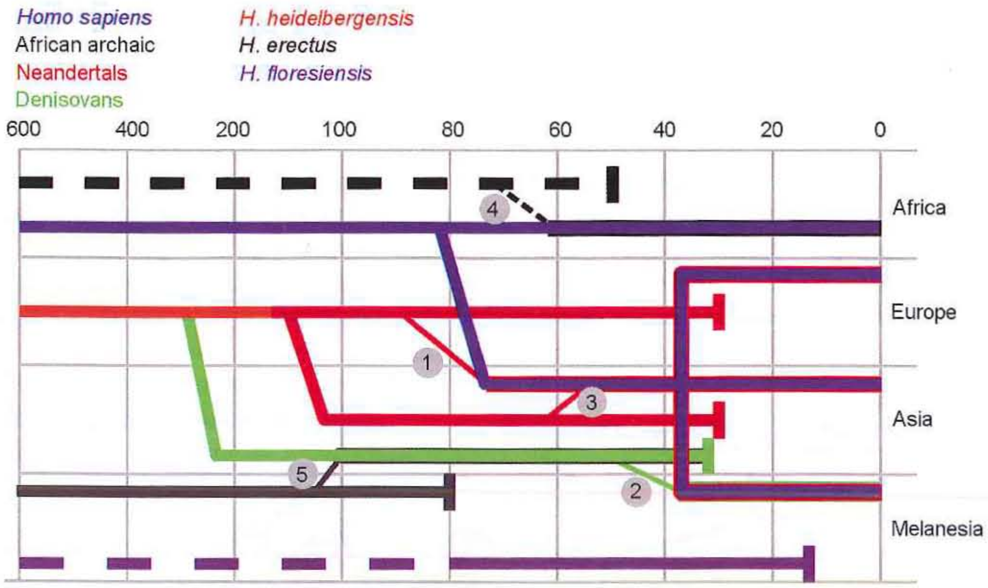

Fig. 2. A model of population history, showing putative cases of interbreeding among hominin groups. The numbering of geneflow events corresponds to Fig. 1.

humans (Krause et al., 2010). It is possible that this represents another case of admixture between Denisovan ancestors with another archaic human group (Reich et al., 2010). In the near future, the combined analysis of the Denisovan and Neandertal high-quality genomes will undoubtedly provide a definitive answer to the question if such an admixture event has taken place.

Thus, the analysis of the archaic genomes has shown that mixture between different archaic genomes and modern human groups occurred at least twice and probably multiple times during human history (fig. 2). It was therefore probably a common occurrence during human history. Thus, the statement by A.P. Derevianko in 2005 "Dear colleagues, please do not offend Neanderthals. They are among our ancestors!" (A.P. Derevianko, 2005) has proved eminently correct.

Conclusion

The approach taken by A.P. Derevianko in his work at Denisova Cave and elsewhere has set a new, high standard for interdisciplinary research into the origin of humankind, by allowing the amount of information extracted from small hominin remains devoid of informative morphological features to be maximized. Even more fundamentally, his work has established Central Asia as the key area for understanding the recent evolutionary history of humans.

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