Introduction

The most important objective of the joint archaeogenetic laboratory of the Institute of Hungarian Research and the University of Szeged is to reconstruct the population history of the Carpathian Basin, during which our initial efforts were focused on exploring the origins of the conquering Hungarians. Since the beginning of our work, we have kept up with methodological developments in the field, as reflected in our scientific publications. In our most recent work, we analysed a large number of samples from the Hun, Avar and conquest periods at the whole genome level. This is considered the most modern and highest resolution investigation given that it analyses the entire hereditary material set, from which it is possible to reconstruct the ancestry relations with high certainty. I will present these results in this paper, but I wish to note at the outset that our previous results from the analysis of maternal and paternal

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1 Marótí et al. 2022
lineages were not contradicted by the genome results, but merely clarified to a considerable extent.

**The origin of the European Huns**

It is most convenient to begin the presentation of the material chronologically, with the Hun period. Given the short duration of the Hun period in the Carpathian Basin (late-4th century AD – mid-5th century AD), the Hun finds are modest in comparison with other periods, and the number of finds that may actually be the legacy of the Huns entering the Carpathian Basin is negligible. To focus our investigations on the latter category, with the help of expert archaeologists we collected remains typically discovered in solitary graves of Mongoloid or mixed anthropological type, along with typical jewellery and weaponry of the period. One of the most important questions of the period is whether the European Huns were related to the Asian Huns (Xiongnu). Fortunately for us, in the 2020 publication by Jeong et al., which outlines the genetic history of Mongolia, among others 60 genomes were published from the Mongolian Xiongnu period (3rd century BC – 1st century AD), providing an excellent benchmark for answering this question.

In this context, it is worth mentioning the oft-heard layman’s objection that kinship with the Huns cannot be genetically proven because there is no “Hun gene”, since the adjective “Hun” does not denote an ethnic group but a political formation. These empires were multi-ethnic and multilingual states forged from many peoples. This sounds convincing because the second half of the statement is true; nevertheless, the first half is false. It is easy to understand why by looking at the example of the Xiongnu genome analyses. In Mongolia, just before the Asian Hun period, two very different human genetic types existed. The western half of Mongolia was inhabited by the descendants of the Asian Scythians of European origin, and the eastern half by the descendants

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2 Jeong et al. 2020
of the ancient Mongoloid Slab Grave culture of Siberian origin. From the studies of Jeong et al.\textsuperscript{3} we know that the two populations intermingled with each other and with on Iranian population from the Turan lowlands in the Xiongnu period, which also mixed with Chinese and Sarmatian populations during the late Xiongnu period. Of course, there is indeed no uniform “Asian Hun gene”, or more correctly “genome type”, but instead there is a large number of genome spectra specific to a particular place and time. In other words, the above admixtures have produced several unique genome formations specific to the Asian Huns that did not appear anywhere else in the world. This is the key reason why genetic relatedness can be established despite genetic diversity, which is made possible by advanced genome analysis softwares. For example, in the Jeong's publication\textsuperscript{4} they were able to identify Chinese, Iranian and Sarmatian admixtures in the Xiongnu, all of which were also descendants of earlier admixtures, because genome analysis algorithms can find the optimal sources of an examined genome from a large number of possible sources and determine admixture proportions. Consequently, genome analyses can indeed answer the question of whether or not the European Hun genomes we are studying can be traced back to any of the known Asian Hun genome types.

After this methodological digression, we can now return to the presentation of our results. From the 9 Hun genomes we analysed, two armed men buried with partial horse remains definitely had Mongolian ancestry, and their genomes corresponded to the genome type that was typical exclusively to the particular Late Xiongnu, which showed a Scythian–Slab-grave–Chinese admixture. What is more, these Carpathian Basin Hun genomes appeared to be almost identical to another European Hun genome (\textit{Kurayly_Hun_380CE}) discovered near the Ural Mountains.\textsuperscript{5} A third Hun genome we studied was found to be an admixture of Xiongnu and local Carpathian Basin ancestry. One other genome from the Hun period was identified by the program as 100% Sarmatian, two others as Sarmatian-local admixtures, and one as an Asian Scythian-local admixture.

\textsuperscript{3} Joeng et al. 2020
\textsuperscript{4} Joeng et al. 2020
\textsuperscript{5} Gnecchi Ruscone et al. 2021
Two further Hun finds were clearly of Gothic-Germanic ancestry. Our results show that some of the European Huns certainly had Asian Hun ancestry, while others were of Sarmatian and Germanic ancestry integrated along the way, which is almost exactly what we would expect based upon the historical sources. Of course, the composition of the European Hun empire was different from that of the Xiongnu, but it inherited its political structure\(^6\), and according to our data, part of its population as well. Importantly from the perspective of further studies, we have identified a specific genome composition that can be traced back to the Xiongnu, but is now specific to the European Huns.

**The origin of the Avars**

The age of the Huns was followed by the Avar period (568-850 AD), and the number of Avar finds excavated in Hungary is very high. The Avar period was very heterogeneous in archaeological and anthropological terms\(^7\), so with the help of archaeologists and anthropologists we have tried to compile a representative sample set including of all the human and archaeological types from the cemeteries excavated in the various regions of the Great Plain. To obtain a realistic picture of the period as a whole, we have analysed 40 samples from the Early Avar period, 33 samples from the Middle Avar period and 70 samples from the Late Avar period, from a total of 35 cemeteries.

The analyses showed that more than a third (55) of the 143 individuals had a distinctly local, European genome, while 88 had varying proportions of Asian heritage, i.e. they could be immigrants or an admixture of immigrants and locals. We have shown that 12 individuals carrying purely Asian genomes, devoid of any European components, descended from the same former population. Of these 12 individuals, 10 were buried in 8 different cemeteries in the Early Avar period, and 4 of them could have been members of the early elite based on the artifacts buried with them. These 12 individuals can be

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6 Kim 2013  
7 Fóthi 2000
considered the prototypes of Avar immigrants and were therefore analysed in detail. Their genome composition clearly indicated an ancient Mongolian origin, and they proved to be descendants of the early Xiongnu. This suggests that the Avars and the Huns were descended from distant common ancestors, but to avoid any misunderstanding, it should be stressed that we are talking here only about the presumably elite strata of Avars and Huns originating from Mongolia.

Of the other 76 individuals carrying Asian ancestry, 26 proved to be an admixture of immigrant Avar elites and the local population in the Carpathian Basin, while a further 9 also had Hun and Iranian components. The analysis showed that the remaining 41 individuals lacked the heritage of the Avar elite, and instead were an admixture of Hun and Iranian ancestry as well as varying proportions of the local population in the Carpathian Basin. The Hun component was identified by our own European Hun samples and the Xiongnu genomes.

The data suggests that the local, migrant Avar and Hun communities were initially well separated by place of residence and burial. For example, no or hardly any Asian genetic traces were found in the cemeteries of Alattyán-Tulát, Homokmégy-Halom, Mélykút-Sáncdülő, Szeged-Makkoserdő, Székkutas-Kápolnadülő and Kiskundorozsma-Kettőshatár-I, and the Szeged-Fehértó-A, Szeged-Kundomb, Kiskundorozsma-Daruhalom, Kiskőrös-Pohibuj-Mackó dülő and Sükösd-Ságod communities were also mainly composed of descendants of local indigenous people. By contrast, the former communities of the Csepel-Kavicsbánya, Kiskőrös-Vágóhídi dülő, Kunpeszér-Felsőpeszér, Csólyospálos-Felsőpálos, Kiskundorozsma-Kettőshatár-II, Tatárszentgyörgy, Madaras-Téglavető, Ároktő-Csík-gát and Felgyő-Ürmös-tanya cemeteries were mainly composed of Avar immigrants. As already mentioned, a third group of Avars was dominated by the Hun heritage, such as the Avar period communities of Makó-Mikócsa-halom, Árkus-Homokbánya, Szarvas-Grexa-Téglagyár, Dunavecse-Kovacsos-dülő and Szegvár-Oromdülő.

In conclusion, the Avars and the Huns were related in two ways. On the one hand, the elites of both immigrant groups came from Mongolia, with early Xiongnu ancestry, and on the other hand, a significant part of the Avar
immigrants were remnants of the former European Hun Empire. Our data suggests that with the arrival of the Avars in Europe, the peoples previously living there were only overlaid by a smaller group arriving from Mongolia. This fits well with the picture of Kim\textsuperscript{8} reconstructed from the historical data, according to which both the Huns and the Avars continued the political structure of the Xiongnu Empire, and the Avars replaced only the leading layer of the former Hun Empire.

The origin of the conquering Hungarians

The Avar era was followed by the arrival of Árpád and his people, the Hungarian conquest. We significantly expanded our pool of samples from the cemeteries of the 10\textsuperscript{th}-11\textsuperscript{th} centuries, analysing 48 genomes from 18 so called “campsite” cemeteries representing the 10\textsuperscript{th} century elite, and 65 remains from 9 so called “village” cemeteries, representing mainly the common people of the 10\textsuperscript{th}-11\textsuperscript{th} centuries. As with the Avars, again we found that almost half of the 113 individuals (48) had local European genomes, while the remaining 53 genomes contained varying proportions of Asian components. The 12 individuals with the highest Asian proportions were shown to have a high degree of genomic similarity, and to belong to the same contemporary population despite being from 9 different cemeteries. Since these 12 individuals can genetically be considered as prototypes of the immigrant conquerors, we analysed their genome composition in detail to shed light on their ancestry.

The genomes of the 12 “conqueror prototypes” most closely resembled those of the Bashkirs and the Volga and Siberian Tatars among the populations living today, confirming the conclusion we had previously drawn from the results of maternal and paternal lineages. Among the ancient populations, the most similar in chronological order were the following: The Bronze Age Okunevo and Karasuk samples excavated in the Minusinsk Basin, the Iron Age

\textsuperscript{8} Kim 2013
Sakas excavated in Kazakhstan, the Asian Scythians excavated in the Tuva-Altai region and in the western part of Mongolia, members of the Sargat culture excavated east of the Urals, and the Xiongnu samples excavated in western Mongolia. These mark a well-defined geographical region, corresponding to the forest-steppe area east of the Ural Mountains, extending as far as the Altai, where the Asian Scythians lived.

As genome similarity alone does not shed light on ancestry, we will now address this issue. We found that the 12 “conqueror prototypes” can be traced back to ancestors common to our closest linguistic relatives, the Mansi (Vogul), the Samoyed-speaking Nganasan, Selkup and Enet peoples. Meanwhile, the highest-resolution analysis (\textit{qpAdm}) showed that the “conqueror prototype” genome can be modelled from 50% Mansi, 35% early or late Sarmatian, and 15% Xiongnu or Asian Scythian genomes. Significantly, only the Sarmatian genomes found in the Ural region fitted the model, besides a few unusual Asian Scythian genomes with a considerable Mongolian Slab Grave heritage. From the genomes we can also determine the dates of the former admixtures: we managed to demonstrate that the Sarmatian admixture occurred between 643 and 431 BC, and the Hun or Scythian admixture between 217 and 315 AD. These results suggest that ancestors of the “conqueror prototype” once belonged to a common ancient population with the ancestors of the Mansi, and that the two peoples separated in the Iron Age. Following this separation, the ancestors of the conquerors mixed with the early Sarmatians to a considerable extent, followed 700 years later by a second mixing, which dates immediately before the European Hun period. This second admixture occurred with the distinctive Scythian–Slab-grave–Chinese genotype, which undoubtedly identifies the descendants of the Asian Huns, but the admixture date was much closer to the European Hun period. Having shown above the genetic continuity between the Asian and European Huns, and moreover, having found in the European Huns this very Scythian–Slab-grave–Chinese admixture genome heritage, it can be stated that the last admixture with the European Huns occurred shortly before they crossed the Volga and were first mentioned in written sources.

Genome analysis also allows for the identification of more distant ancestors, so this issue was investigated too. The result has shown that the common
ancestors of the Mansis and the “conqueror prototype”, which can now be called “proto-Ugric” on the basis of linguistic models, originated from an almost 50/50 admixture of the Late Bronze Age Mezhovskaya culture and the ancestors of the Nganasans (a group of Samoyeds). The Mezhovskaya were the dominant culture of the Late Bronze Age in the forest-steppe zone of the southern Urals between 1300 and 700 BC, but their territory extended from the European side of the Urals to the Altai, and their members are considered by many researchers to be ancestors of the Ugric people. The Mezhovskaya strand points to the same area in northern Kazakhstan as the other genome analyses. In addition, Mezhovskaya is archaeologically linked to the earlier Karasuk culture, so the similarity of the Karasuk genomes to those of the examined conquerors cannot be coincidental either. Both Bronze Age peoples practised mixed farming with crop production, fishing, hunting and animal husbandry, and the horse played a prominent role in their way of life.

The distant past of the “conqueror prototype” can be placed in an even broader context based on the known genome data. The Asian Scythians have previously been shown to be descended entirely from an admixture of the Middle Bronze Age Sintashta-Andronovo population of European descent and the indigenous Siberian population of Asian descent. Since the Mezhovskaya population is also of Sintashta-Andronovo descent, and the Nganasans are an ancient Siberian population, the early history and geographic location of the “conqueror prototype” coincides with that of the Asian Scythians. In other words, their Iron Age ancestors may have formed a group of Asian Scythians.

Now that we have the genome history of the 12 “conqueror prototypes”, let us examine the 53 other individuals who also carried eastern genome components. Since most of these represented the population of village (commoner) cemeteries of the 10th-11th centuries, we hypothesised that they may have originated from an admixture of immigrants and the local indigenous population of the Carpathian

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9 Koryakova and Epimakhov 2007  
10 Narasimhan et al. 2019; Gnechi and Ruscone et al. 2021  
11 Allentoft et al. 2015
RELATIONS AMONG THE HISTORICAL POPULATIONS OF THE CARPATHIAN...

Basin. The analysis showed that the genomes of 31 individuals could indeed be modelled well as an admixture of the 12 “conqueror prototypes” and the local people, while 5 samples also contained Hun and Iranian components. In the remaining 17 individuals, however, the program found no traces of “conqueror prototype” heritage, instead showing them to be of Hun or Avar descent, with varying degrees of Iranian and local admixtures. Most of these belonged to the population of the “campsite” (elite) cemeteries.

The results show that, like the Avars, the conquering Hungarians were also heterogeneous in their composition. The majority of them came from the population of the “conqueror prototype”, but they were also joined by a significant proportion of the population of the former Hun and Avar empires. Some of them may have united with the Hungarians before the conquest, while the rest did so in the Carpathian Basin. The conquering Hungarians were also related to the Huns in two ways. On the one hand, they mixed with the Huns in their ancestral homeland between 217 and 315 AD, and on the other hand, they integrated a significant proportion of Hun descendants. One of the most striking pieces of evidence for this is that the father of individual K2-61 excavated in the Karos-2 cemetery was the individual K1-3286 of Hun origin excavated in the Karos-1 cemetery, while his mother belonged to the “conqueror prototype”. Our data suggests that the conquerors also integrated the local population very effectively, as evidenced directly by the fact that the daughter or sister (SH-3) of the individual (SO-5) excavated in the Sárrétudvari-Őrhalom campsite cemetery was buried in the neighbouring Sárrétudvari-Hízóföld village cemetery.

**Summary**

The large sample size and careful sampling of the Avar and conquest-period genomes we have analysed certainly provide a good representation of the population composition of the two periods. This is why we can say that our high-resolution genome analyses have reconstructed the population history of these periods to the highest accuracy currently available. We have successfully
identified groups representing the immigrant elite from both periods, and have traced their most likely origins back to the Bronze Age. Our data showed that the local European Bronze Age population outnumbered the immigrants in both periods. This can also be said for the Hun period, despite the fact that here the purposive sampling was primarily directed at immigrants. Our results also help to answer a number of questions that have been debated until now. The biological continuity demonstrated between Asian and European Huns confirms the continuity between the two ethnic groups and the two empires, which has been questioned until now. The Mongolian origins of the Avar elite support the theory of their Juan-Juan origin. The high degree of overlap between the populations of the Avar and Hun periods may explain why the Avars are absent from the Hungarian chronicles. Our data also shows that the ancestors of the conquerors always lived in the forest-steppe and steppe zones, and that the Mansi moved to their northern habitat after the Iron Age split, as had been indicated by the common Ugric vocabulary for horse-keeping\textsuperscript{12} and the mythological traditions of the Mansis concerning the horse\textsuperscript{13}. Our data confirms the relationship of the Hungarians with the Huns, which may provide historians with new evidence to reassess their earlier doubtful position\textsuperscript{14}. The history of the conquerors reconstructed back to the Bronze Age may also help to clarify previous linguistic hypotheses, for example, the Iranian-origin loanwords\textsuperscript{15} in the Hungarian language may be linked to the Sarmatians, while the earliest Turkish loanwords\textsuperscript{16} may well be attributed to a contribution from the Huns.

\textsuperscript{12} Zaicz et al. 2006
\textsuperscript{13} Napol'skikh et al. 2008
\textsuperscript{14} Rady 2018
\textsuperscript{15} Abondolo 1998
\textsuperscript{16} Róna-Tas et al. 2011
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Hungarian flag from the Konigsfelden Monastery, 1st half of the 14th century, Bernisches Historisches Museum, Berne. Photo N. Frey