DISPATCH

Historical human migrations: From the steppe to the basin

Many migrations during human history have made the Carpathian Basin the melting pot of Europe. New ancient genomes confirm the Asian origin of European Huns, Avars and Magyars and huge within-group variability that is linked with social structure.

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Prehistoric and historic migrations are the common ingredient in the archaeology of the Carpathian Basin, a region of Central Europe encompassing today's Hungary as well as parts of neighboring countries. The Mesolithic hunter-gatherer colonization^{1,2}, the introduction of agriculture in the Early Neolithic³, the rise of the Bronze Age society^{4,5} and finally, the constitution of historical ethnicities before, during and after the fall of the Roman Empire⁶ are just a few of the many migration-linked processes making the Carpathian Basin the melting pot of Europe. Historically, the appearance of Huns, Avars, and Magyars in the Carpathian Basin between the fourth and ninth centuries is considered to be the result of subsequent large-scale migrations of ethnic groups periodically establishing political control leading to the rise of the first states^{7,8}. In light of political instrumentalization of ethnic categories in past research, archaeologists use the same names as chronological designations to label similar material culture assemblages and practices⁹. By contrast, in ancient DNA studies, individuals are assigned into groups based on associations inferred from their archaeological or historical context as there is usually no

alternative that would be biologically more informative. However, it is important to keep in mind that sharing the same archaeological context does not necessarily mean that the individuals form a single genetic population. Finding out if a cultural affiliation or ethnicity of the past can be linked to a single or several distinguishable genetic populations is one of the goals of ancient DNA studies. Given the scarcity of historical sources and the richness of the archaeological record, population genetics can provide further insight into the complexities obscured by ethnic labels. This is due to a focus on the characterization of demographic processes, such as migration and subsequent admixture or (partial) isolation due to differences in social rank or genetic background. Two new studies — one in this issue of *Current Biology* by Zoltán Maróti, Tibor Török and colleagues¹⁰, and another by Guido Alberto Gnecchi-Ruscone and colleagues¹¹ — analyze genome-wide ancient DNA data from a total of 337 individuals primarily from the Migration Period Carpathian Basin, shedding light on the migrations and admixture processes of Huns, Avars and Magyars.

The genomes of most modern-day Europeans consist of various proportions derived from three main ancestral groups of people⁴: local Mesolithic hunter-gatherers¹, early farmers from Anatolia whose ancestry can in turn be traced back to the Levant³ and Yamnaya-culture-associated pastoralists from the East European steppe^{4,5}. This is also true for modern Hungarians whose genomes are composed mostly of steppe and early farmer ancestries with a smaller proportion of the hunter-gatherer component, similar to their geographic neighbors⁴. In addition, a connection in the form of a shared minor Y-chromosome haplogroup has been identified between Hungarians and populations in West Siberia, including their closest language relatives Mansis and Khantys¹², belonging to the Ugric branch of the Uralic language family which is found in Northern Eurasia, with the exception of Hungarian. However, it has thus far not been possible to find such a connection at the genome-wide level¹³. Nevertheless, the elusive link between language relatives and other genetic influences that have not left a trace in extant genomes might become apparent when ancient genomes are analyzed. In recent years, hundreds of ancient genomes from Central Asia, China and Mongolia have been published¹⁴⁻¹⁷, making it possible to discern Asian genomic signatures in ancient European populations.

Historically, the Avars were assumed to be a group of steppe people fleeing the destroyed Rouran Khaganate, who conquered the Carpathian Basin in the late 6th c. CE and formed a political organization – khaganate – which lasted until the early 9th c. CE^{7,9,11}. One of the main scientific challenges was their origin — Avars left no direct written sources and the history of their appearance in the Carpathian Basin was secondarily reported in Byzantine writings, which included information about multiple Avar groups or even the possibility of a fraudulent identity^{7,10,11}. However, given the richness of archaeology from this period, the label 'Avar' was still applied to the overall achievements of people in the Carpathian Basin during this period^{7,9,18}. The major increase in settlement activity (c. 600 sites) and burial practices (c. 100,000 graves)^{9,11} in the Carpathian Basin displayed a complex network of interaction including steppe, Mediterranean and Byzantine influences. In terms of social structure, richly furnished graves accompanied by horse burials suggest that the Early Avar elites (Figure 1) emphasized their steppe origins during burial ceremonies to differentiate themselves from other inhabitants of the Carpathian Basin^{9,18,19}. These lavish burial practices strongly contrast with numerous burials without grave goods^{9,18,19}.

Maróti and colleagues¹⁰ present shotgun sequencing data from 143 Avar period individuals from the sixth to the ninth century, while Gnecchi-Ruscone and colleagues¹¹ analyze in-solution enrichment data from 48 individuals from the same period. When combining their results, it appears that Avars were a genetically heterogeneous group whose ancestry profiles reflect geographic and social structure. Individuals whose rich burial assemblages are suggestive of them belonging to the elite show high proportions of "ancient Northeast Asian" (ANA) ancestry and are genetically most similar to Rouran²⁰, Xianbei¹⁴ and Xiongnu¹⁵ individuals from Mongolia^{10,11}. This is especially true for early elite individuals from the core area of the Avar empire (Danube–Tisza Interfluve), while later individuals show some additional Western Eurasian ancestry¹¹. Non-elite Avar individuals display a wide range of ancestry profiles, ranging from fully European to predominantly Northeast Asian (identical to the elite)¹⁰. Furthermore, individuals from regions surrounding the Avar core area are particularly heterogenous¹¹ with some having greater affinity to

Xiongnu or Hun period individuals than to the Avar elite¹⁰, indicating a more complex history of admixture. Recent admixture dates of individuals from the peripheral areas¹¹ suggest outgroup marriage during the Hunnic and Early Avar periods as a potential cause of the heterogeneity.

In addition to Avars, Maróti and colleagues¹⁰ also studied preceding and succeeding occupants of the Carpathian Basin, in particular the earlier Huns and later Magyars.

Archaeologically, the relatively short duration of the Hun Empire in the Carpathian Basin in the 5th c. CE was accompanied by rapid changes in material culture, which included the succession of multiple regional styles over the course of a single century, as well as the introduction of new artefacts such as new pottery types, ornaments including brooches or buckles, knives and weapons^{10,11}. The variety of artefacts and their geographic origins point to the complexity of demographic and cultural dynamics of the Migration Period, reflecting the heterogeneity of the inhabitants^{10,11}. aróti and colleagues¹⁰ show that the genomes of European Huns vary from western (European) to eastern (Northeast Asian) similar to Avars, with individuals with the easternmost affinities genetically sharing the most with Mongolia-related groups (Xiongnu, Xianbei).

The arrival of Magyars from the east in the Carpathian Basin in the ninth century and their rapid conquest earned them the moniker 'conquerors'^{8,10,12}. Similarly to Avars, the succeeding Magyar elite maintained steppe traditions, burying their dead with steppe-related artifacts with some sites including horse burials^{8,10}. The long-term impact of their presence, beyond the assumed origins of the Hungarian nation, has raised questions regarding the impact on the local population and the subsequent changes with the introduction of Christianity in the tenth and eleventh centuries, when steppe-related practices decline¹⁰. Magyars also present a west-to-east ancestry cline like Huns and Avars¹⁰, however failing to reach as far east and the individuals in its easternmost extent have ancestry from Late Bronze Age Southern Urals⁵, Siberia (modern Nganasans as proxy) and Late Bronze Age Altai-Mongolian region^{16,17}. Notably, elite individuals display more similarity to Asian whereas non-elite individuals to European genomes¹⁰. What is more, individuals from

certain cemeteries derive ancestry from Asian-like Xiongnu/Huns/Avars instead of Asian-like Magyars¹⁰.

Maróti and colleagues¹⁰, as well as Gnecchi-Ruscone and colleagues¹¹, have provided genetic evidence of several migration events into the Carpathian Basin from the east, resulting in ethnic groups encompassing at least two genetic populations that partially admix with each other. Further evidence of ties between the Carpathian Basin and broadly Central-Eastern Asia reveals the importance of framing long-term historical developments as a complex transect of cultural change. By shifting the focus from the elites to the commoners, the results highlight the asymmetrical consequences of Hunnic, Avar and Magyar migrations – gene flow was mostly unidirectional from the migrant elite to the local commoners, especially in the early stages of admixture¹¹. This sparks interest in the dynamics of social developments and accompanying cultural change. Further questions include when, why and how have the relatively extensive eastern genetic influences disappeared from the genomes of present-day Hungarians. This is especially interesting as the modern Hungarians have retained their language, despite being geographically isolated from other Uralic-speaking populations in the northeast. Future interdisciplinary studies will hopefully shed light on these topics and potentially even answer questions that we have not known to ask.

Declaration of interests

The authors declare no competing interests.

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Figure 1. A richly furnished Avar elite burial.

An early 7th century elite Avar male burial discovered in Szalkszentmárton (Danube-Tisza Interfluve)¹⁹. The burial rite involving animals (partial horse and sheep burials), as well as grave construction point towards funerary practices of Eastern Hungary, while the richness of grave goods is characteristic for the local Kunbábony group^{15,17,19}. Burial and selected artifacts – left: two belt fittings; center: the burial and the distribution of finds; right: a sword and a stirrup¹⁹ (images by Bernadett Kovacsóczy).