PhD DISSERTATION'S THESES

The origin and composition of the "Forgotten people": genetic analysis of the Sarmatian-period population of the Carpathian Basin

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I. Introduction

Archaeogenetics is the study of the genetic material of long deceased individuals. By studying the genetic composition of historical populations, we can make valuable inferences regarding their geographical origin, distribution, their movement and possible connections with each other. Although the interpretation of these data depends heavily on interdisciplinary collaboration of several independent research fields (e.g. histography, archaeology, linguistics, anthropology), archaeogenetics provides insights that were previously unattainable through more conventional approaches to the study of human history.

A long-term goal of the archaeogenetics community is to reconstruct and understand the population genetic history of the Carpathian Basin. In pursuit of this, previous studies have focused on key demographic events such as the initial Neolithic expansion into the region (7th millennium BCE) as well as major transformations during the Bronze Age (3rd to 1st millennia BCE). More recent research has provided detailed insights into later periods, including the Avar (~7th-9th centuries CE) and Hungarian Conquest (~9th-10th centuries CE) Periods. Despite these advances, a significant gap remains in our knowledge of the region's demographic history, particularly regarding the Iron Age and the Roman occupation periods, from which genetic data are still scarce. In this study, we aim to address this gap by investigating a major population from the Roman-era Carpathian Basin, the Sarmatians, who occupied its eastern part, beyond the direct control of the Roman Empire.

The Sarmatians were a group of nomadic people who likely originated in the southern Ural region during the 4th-2nd centuries BCE. In the subsequent centuries, they gradually expanded into the Pontic Steppe territories, displacing the culturally related Scythians. According to historical sources, they also migrated into the Carpathian Basin around the middle of the first century CE, first settling in the Danube-Tisza interfluve, then expanding eastward to occupy the whole of the Great Hungarian Plain.

The populations migrating from the steppe into the Carpathian Basin quickly adapted to local conditions, abandoning their nomadic lifestyle and adopting agricultural and artisanal activities. This transition is evidenced by numerous archaeological findings and the extensive settlement network that developed on the Great Hungarian Plain.

Although the Sarmatians initially maintained good relations with the Roman Empire, they allied with the Germanic tribes during the Marcomannic Wars (166–180 CE). Following the extensive campaigning of Emperor Marcus Aurelius, they were decisively defeated and received harsh peace terms including forced conscription. After this however, their relationship with the Roman Empire improved significantly. Furthermore, as the Empire sank into the turmoil of the 3rd century, the Sarmatians have prospered as evidenced by the influx of imported roman goods as well as the documented presence of lucrative trade routes crossing over the Great Hungarian Plain. By the 4th century, renewed waves of migration into the region reignited tensions. Hostilities between the Sarmatians and the Roman Empire flared up along the Danube limes, leading to economic disruption on both sides of the border.

The relative independence of the Sarmatians came to an end around the turn of the 4th to 5th centuries CE, when the newly arriving Huns took control of the region and established their power centre in the Carpathian Basin. Although the Sarmatians gradually disappeared from the historical records, it is unlikely that their entire population vanished. More plausibly, they were gradually assimilated into the population of the subsequent Gepid Kingdom.

Interestingly, this once-dominant people, who ruled over a vast region and significantly influenced the ancient and early medieval world (military innovations, relations with the Roman Empire) are not claimed as ancestors by any modern European state-forming nations and remain a group of ancient, now forgotten people.

II. Objectives

Given the length of their occupation and the considerable size of their population (evidenced by an extensive settlement network and numerous excavated burials) the Sarmatians represent a significant chapter in the population history of the Carpathian Basin. To investigate the genetic composition of this important group, we employed traditional genome-wide variance analysis to address broad questions, complemented by a state-of-the-art IBD (identity-by-descent) fragment detection method to identify distant genealogical relationships with high confidence.

The primary aims of our study were as follows:

- Characterize the genetic composition of the Sarmatian-period population of the Carpathian Basin.
- 2. Investigate the relationship between the Iron Age steppe nomads and the people found in the Carpathian Basin identified as Sarmatians.
- 3. If a connection exists, try to reconstruct the migration path the Sarmatians took to reach the Carpathian Basin.
- 4. Assess the genetic impact of the Sarmatians during their occupation and in subsequent periods of the Carpathian Basin's population history.

III. Materials and Methods

Sample collection and classification

The vast number of excavated burials has enabled us to conduct high-resolution sampling across distinct periods associated with the Sarmatian occupation of the Carpathian Basin. We collected and sampled 244 human remains in total. Following the archaeogenetic preparation of the samples we were able to obtain whole genome sequences in 156 cases. Of these, 17 samples were obtained from Wallachia and Moldavia (historical regions in present-day Romania), from outside the Carpathian

range to explore potential traces of Sarmatian migration. Additionally, 21 samples were collected from the subsequent Hun Period to investigate the potential continuity of the Sarmatian-period population and to contextualize the genetic composition of the Migration-period population. We complemented this sample set with 26 publicly available genomes to obtain the most comprehensive genome database representing the population of the Carpathian Basin between the 1st-5th centuries AD.

The samples were thoroughly reviewed for precise archaeological classification. We also performed radiocarbon measurements in 68 cases to anchor and validate the archaeological evaluations. We adopted a refined periodization of the Sarmatian occupation period mainly based on the existing archaeological conventions, and we classified our samples into these chronological phases where the archaeological and radiocarbon dates supported each other. These phases included:

- Western Steppe Sarmatian Period
- Carpathian Basin Early Sarmatian Period
- Carpathian Basin Early-Middle Sarmatian Period
- Carpathian Basin Middle-Late Sarmatian Period
- Carpathian Basin Late Sarmatian Period
- Carpathian Basin Sarmatian Unknown Period
- Carpathian Basin Late Sarmatian-Hun Period
- Carpathian Basin Hun Period

DNA preparation

DNA preparations were carried out at the dedicated ancient DNA laboratory of the Department of Genetics, University of Szeged according to established protocols. The prepared libraries were shallow sequenced on Illumina iSeq 100 platform to monitor their human DNA content. Selected libraries were deep sequenced on the Illumina NovaSeq 6000 platform to an intended average coverage of 2-3X.

Data processing and quality control

The raw sequencing reads were aligned to the Genome Reference Consortium Human Build 37 (hs37d5). Ancient DNA damage patterns and contamination levels were carefully monitored to ensure data authenticity and quality. The aligned nucleotide sequence data was deposited to the European Nucleotide Archive (accession no. PRJEB80732).

Genome-wide variance analysis

We conducted traditional genome-wide variance analysis methods to investigate the underlying genetic structure of the Carpathian Basin Sarmatians as well as to test specific hypotheses.

The hypothesis-independent PCA (Principal Component Analysis) analysis was used to project our samples onto the genetic variance landscape defined by an extensive background of 1397 modern individuals from 179 contemporary Eurasian populations. We also applied the unsupervised ADMIXTURE analysis frameworkusing exclusively ancient genomes as additional references - to model our genomes as compositions of hypothetical ancestral populations.

We also employed multiple F-statistics based approaches – namely F4-statistics and qpAdm - to statistically evaluate the possible genetic connection between the Carpathian Basin Sarmatians and publicly available Sarmatians excavated in the Southern Ural region and Kazakhstan.

Discrete, haplotype-based analysis

To explore the genetic connectedness at a deeper level, we conducted haplotypebased analyses at both the individual and population levels.

We selected and imputed a total of 562 ancient genomes (including our own samples) applying strict quality thresholds to ensure reliability. Following this, we applied the ancIBD framework, supplemented with a novel filtration method, to

identify shared genomic segments of at least 8 cM in length. These segments were confidently assigned as IBD (identity-by-descent) fragments, indicating genuine genealogical relationships among the analysed individuals.

In addition, we determined mitochondrial and Y-chromosome haplogroups for our samples using established open-source software tools. To better understand the likely origins of these uniparental lineages, we compiled a comprehensive reference database encompassing 972 publicly available ancient individuals from the Carpathian Basin.

IV. Results and Discussion

1. The Sarmatians of the Carpathian Basin can be derived from the Sarmatians excavated on the Russian and Kazakh steppes (henceforth Steppe Sarmatians).

The PCA and ADMIXTURE analysis indicated that most of the Carpathian Basin Sarmatians display distinct genetic composition compared to the Steppe Sarmatians, aligning more closely with the preceding and contemporary populations of the Carpathian Basin. However, the ADMIXTURE analysis indicated a small but substantial East Asian-related genetic fraction which was present in the majority of individuals separating them from other populations of the region.

F4-statistics confirmed that this East Asian affinity was indeed present in the indicated samples. Furthermore, this component was shown to be adequately modelled from Steppe Sarmatian sources using both F4-statistics and qpAdm.

Analysing the IBD sharing among our extensive ancient Eurasian whole-genome database also confirmed these results. The Sarmatians of the Carpathian Basin formed a distinct cluster in simple graph-based ordering approaches, while the Steppe Sarmatians occupied a central position within this Sarmatian cluster. Further IBD count-based analyses showed that the Steppe Sarmatians share a substantial amount of IBDs with the different Carpathian Basin Sarmatian groups and this connection seemed to gradually decline throughout the progressive periods. This

indicated a possible founding effect originating from the Steppe Sarmatians with a continual chain of generational transmission.

Focusing specifically on close genealogical connections, we were able to identify an extended family of Steppe Sarmatian individuals that spanned the full duration of the Sarmatian occupation across the Steppe region, both spatially and temporally. Remarkably, this family also included several individuals sequenced in our study, among them 3 Sarmatians from Romania and 1 Early Sarmatian from the northern edge of the Great Hungarian Plain.

Together, these show that the Carpathian Basin Sarmatians indeed descended from the Steppe Sarmatians, although their steppe ancestry has been strongly depleted probably due to a small initial population size or a stepping-stone migration pattern which already incorporated "local" elements outside the Carpathian Basin.

2. Population level IBD analysis reveals several potential migration events.

By applying IBD analysis at the population level, we identified demographic patterns that would have remained undetected using traditional methods.

When comparing the normalized ratio of IBD sharing across the different Carpathian Basin Sarmatian groups, a pronounced gap in the generational transmission emerged during the Early-Middle Sarmatian Period. This discontinuity suggests a migration event involving groups from Northern Europe and Central Asia, distinct from the previously identified Steppe Sarmatian sources, a pattern also supported by PCA and qpAdm analyses.

Additionally, when recalculating IBD sharing based on cemetery-level groupings, we observed a marked reduction in IBD connectivity in approximately half of the Late Sarmatian and Hun-period cemeteries, relative to earlier phases. This pattern again suggests a migration event, with qpAdm results pointing to a possible origin in Southern Europe or the Balkans.

3. Individuals from the Hun Period can be described as mostly continuous with the previous Sarmatian Period population.

The majority of the Hun-period individuals showed identical genetic composition to the previous Sarmatian-period population both on PCA and ADMIXTURE. However, several outliers with strong East Asian affinity were also identified.

Graph-based IBD analyses revealed that Hun-period individuals do not form a distinct IBD cluster. Instead, they are dispersed across individuals from both earlier and later periods. A more detailed examination of IBD sharing within the Hun Period mirrors the PCA results, revealing two distinctly separated IBD-sharing clusters: one composed primarily of Avar-period samples, including a few Conqueror elites; the other dominated by Sarmatian-period individuals, notably including several Romanian and Steppe Sarmatians, with minimal connections to Roman, Avar, or Conquest-period groups.

Together, these findings suggest that the archaeological classification of this group may be somewhat artificial. While the genetic data clearly reflect the presence of new migrants, the majority of Hun-period individuals show strong genetic and genealogical continuity with the preceding Sarmatian population.

4. IBD data indicates at least a partial survival of the Sarmatian and Hunperiod population.

According to our group-based IBD analysis both the Sarmatian and Hun-period group projected a low but detectable ratio of IBD connections toward the much later Avar and Conquest-period populations, indicating at least partial survival across these transitions.

5. Uniparental data strongly suggests male-biased migration.

Haploid data analysis showed a very apparent turnover in the Y-chromosome haplogroup distribution of the Sarmatian-era population of the Carpathian Basin. The characteristic Central Asian haplogroup R1a-Z94, which had been only

sporadically present in earlier periods, emerged suddenly in this era. It was also the most common Y-haplogroup among Steppe Sarmatian males and in our Romanian Sarmatian samples, highlighting a strong unifying paternal signal across all Sarmatian groups. In contrast, the maternal haplogroup distribution showed less coherence. While many maternal lineages found among the Steppe Sarmatians are also typical of Central Europe, a notable proportion of Asian-derived mitochondrial haplogroups was present among them. These however were largely absent in both the Carpathian Basin and Romanian Sarmatian samples. A significant shift in maternal lineages only became evident after the Sarmatian Period and particularly during the much later Avar Period. Taken together, these findings suggest that the Sarmatian migration was predominantly male driven.

V. Summary

In summary, we show that the Carpathian Basin Sarmatians descended from Steppe Sarmatians originating in the Ural and Kazakhstan regions, with Romanian Sarmatians serving as a possible genetic bridge between the two groups. However, the steppe-derived ancestry observed in the Carpathian Basin appears significantly diluted, likely due to substantial local admixture or the migration of groups that were already genetically admixed prior to their arrival. We also identify two previously unknown migration waves during the Sarmatian era and a notable continuity of the Sarmatian population into the Hun Period, despite a smaller influx of Asian-origin individuals. Furthermore, we observed a substantial increase in the frequency of the characteristic Central Asian paternal haplogroup R1a-Z93 during the Sarmatian Period in the Carpathian Basin. This shift was not mirrored by a corresponding change in the distribution of maternal lineages, possibly pointing toward a male driven migration. These results shed new light on Sarmatian migrations and the genetic history of a key population neighbouring the Roman Empire.

VI. Összefoglaló

Kutatócsoportunk hosszú távú célja a Kárpát-medence populációtörténetének rekonstrukciója. Az elmúlt években több tanulmány látott napvilágot, amelyek a térség későbbi történelmi időszakaira, különösen az avar és a honfoglalás kori népességre fókuszáltak. Ezzel szemben a vaskorból és a római birodalom korából szinte alig állnak rendelkezésre minták, mely egy komoly hézagként jelentkezik a demográfiai folytonosságban. Ezt a hiányt kívántuk legalább részben pótolni azzal, hogy 156 szarmata és hun kori egyénből állítottunk el teljes genom szekvenciát, akik a Kárpát-medence keleti felének római kori népességét reprezentálják.

Összefoglalásként kimutattuk, hogy a Kárpát-medencében feltárt szarmata kori népesség jelentős része az oroszországi és kazak steppén feltárt szarmatáktól származtatható. Útjuk során, és főként a Kárpát-medencében a steppei genetikai örökségük jelentősen lecsökkent, valószínűsíthetően a helyi népekkel való keveredésük következtében. A részletes IBD elemzés révén két további bevándorlási eseményt is azonosítottunk, valamint kimutattuk a Kárpát-medencei szarmaták jelentős mértékű továbbélését a hun korszakban és legalább részleges továbbélését a jóval későbbi avar és honfoglalás korokban. Az anyai és apai vonalak összehasonlítása a szarmaták lehetséges férfi többségű vándorlására utalt, mivel a korszakban az apai vonalak aránya jelentős változást mutatott (a közép ázsiai R1a-Z93 apai haplocsoport hirtelen megjelenésével), mely azonban az anyai vonalak eloszlásán nem volt megfigyelhető. Eredményeink új adatokat szolgáltatnak a Kárpát-medence populáció történetének egy meghatározó szeletéről és egy olyan jelentős népességről, mely napjainkra sajnálatos módon feledésbe merült.

VII. Publications

MTMT identifier: 10078234

Publications relevant for the doctoral procedure:

Schütz, O., Maróti, Z., Tihanyi, B., Kiss, A. P., Nyerki, E., Gînguță, A., Kiss, P., Varga, G. I. B., Kovács, B., Maár, K., Kovacsóczy, B. Ny., Lukács, N., Major, I., Marcsik, A., Patyi, E., Szigeti, A., Tóth, Z., Walter, D., Wilhelm, G., ... Török, T. (2025). Unveiling the origins and genetic makeup of the "forgotten people": A study of the Sarmatian-period population in the Carpathian Basin. Cell, S0092867425005598. https://doi.org/10.1016/j.cell.2025.05.009

IF: 45.5

Maróti, Z., Neparáczki, E., <u>Schütz, O.</u>, Maár, K., Varga, G. I. B., Kovács, B., Kalmár, T., Nyerki, E., Nagy, I., Latinovics, D., Tihanyi, B., Marcsik, A., Pálfi, G., Bernert, Z., Gallina, Z., Horváth, C., Varga, S., Költő, L., Raskó, I., ... Török, T. (2022). **The genetic origin of Huns, Avars, and conquering Hungarians.** Current Biology, 32(13), 2858-2870.e7. https://doi.org/10.1016/j.cub.2022.04.093

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Other publications:

Kovács, B., Gînguţă, A., Kiss, P., Maár, K., <u>Schütz, O.</u>, Varga, G. I. B., & Neparáczki, E. (2025). **Comparing the Efficiency of Different Methods for Reliable Results in Ancient DNA NGS Workflow.** DNA, 5(2), 26. https://doi.org/10.3390/dna5020026

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Spekker, O., Attila Kiss, P., Kis, L., Király, K., Varga, S., Marcsik, A., <u>Schütz, O.</u>, Török, T., Hunt, D. R., & Tihanyi, B. (2024). White plague among the "forgotten people" from the Barbaricum of the Carpathian Basin – Cases with tuberculosis from the Sarmatian-period (3rd-4th centuries CE) archaeological

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Tihanyi, B., Maár, K., Kis, L., Gînguță, A., Varga, G. I. B., Kovács, B., Schütz, O., Pálfi, G., Neparáczki, E., Török, T., Spekker, O., Maróti, Z., & Berthon, W. (2024). **But no living man am I': Bioarchaeological evaluation of the first-known female burial with weapon from the 10th-century-CE Carpathian Basin.** PLOS ONE, 19(11), e0313963. https://doi.org/10.1371/journal.pone.0313963

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Nyerki, E., Kalmár, T., <u>Schütz, O.</u>, Lima, R. M., Neparáczki, E., Török, T., & Maróti, Z. (2023). **correctKin: An optimized method to infer relatedness up to the 4th degree from low-coverage ancient human genomes.** Genome Biology, 24(1), 38. https://doi.org/10.1186/s13059-023-02882-4

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Gînguță, A., Kovács, B., Schütz, O., Tihanyi, B., Nyerki, E., Maár, K., Maróti, Z., Varga, G. I. B., Băcueț-Crișan, D., Keresztes, T., Török, T., & Neparáczki, E. (2023). Genetic identification of members of the prominent Báthory aristocratic family. iScience, 26(10). https://doi.org/10.1016/j.isci.2023.107911

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Gînguță, A., Kovács, B., Tihanyi, B., Maár, K., <u>Schütz, O.</u>, Maróti, Z., Varga, G. I. B., Kiss, A. P., Stanciu, I., Török, T., & Neparáczki, E. (2022). **Maternal Lineages of Gepids from Transylvania.** Genes, 13(4), 563. https://doi.org/10.3390/genes13040563

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Cumulative IF: 100.7

Book chapters:

Schütz, O., Maróti, Z., Neparáczki, E., Tihanyi, B., Kovács, B., Maár, K., Varga, G., Gînguţă, A., Nyerki, E., Török T. (2024). **Preliminary genetic results on the Sarmatians from the Carpathian Basin.** In: Lavinia, Grumeza; Victor, Cojocaru; Cristina, I. Tica (szerk.) The Sarmatians and the Others: Nomadic and Sedentary Cultures in Central and Eastern Europe in the First Half of the 1st Millenium AD, Cluj-Napoca, Románia: Mega Könyvkiadó pp. 473-481., 9 p.

Maár Kitti, Varga Gergely István, Kovács Bence, <u>Schütz Oszkár</u>, Tihanyi Balázs, Nyerki Emil, Raskó István, Pálfi György, Maróti Zoltán, Neparáczki Endre, Török Tibor (2022). **A X-XI. századi Kárpát-medencei köznép anyai vonalainak jellemzése archeogenetikai módszerekkel.** In: Nagy, Dóra; Nagy-L., István (szerk.) A Magyarságkutató Intézet évkönyve 2021 Budapest, Magyarország: Magyarságkutató Intézet, 542 p. pp. 281-309., 29 p.

Conference presentations:

A) International conferences

Schütz Oszkár, Maróti Zoltán, Kiss P. Attila, Tihanyi Balázs, Alexandra Gînguță, Kovács Bence, Maár Kitti, Kiss Petra, Varga Gergely, Török Tibor (2025). Archaeogenetic investigation of the Gepid Period population of the Carpathian Basin. In: Hungarian Molecular Life Sciences 2025. Eger, Hungary (oral presentation)

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Oszkár Schütz, Emil Nyerki, Endre Neparáczki, Zoltán Maróti, Balázs Tihanyi, Alexandra Gînguță, Attila P. Kiss, Bence Kovács, Kitti Maár, Gergely Varga, Tibor Török (2023). **Preliminary genetic results from the Sarmatians of the Carpathian Basin.** In: 4th Conference of the Török Aurél Anthropological Association: Typical vs Atypical Human Burials in Central and Eastern Europe. Marosvásárhely, Romania (oral presentation)

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B) Local conferences

Schütz Oszkár, Maróti Zoltán, Kiss P. Attila, Tihanyi Balázs, Nyerki Emil, Alexandra Gînguță, Kovács Bence, Maár Kitti, Kiss Petra, Varga Gergely, Török Tibor (2025). A Kárpát-medence szarmata kori populációjának archeogenetikai vizsgálata. In: FIATAL RÓMAI KOROS KUTATÓK XVII. KONFERENCIÁJA. Pécs, Hungary (oral presentation)

<u>Schütz Oszkár</u> (2023). **Az Avar genetikai eredete.** In: I. Medievisztikai Vándorkonferencia. Szeged, Hungary (oral presentation)

<u>Schütz Oszkár</u> (2023). **Előzetes genetikai eredmények a Kárpát-medencei szarmatákból.** In: XI. Eötvözet Konferencia. Szeged, Hungary (oral presentation)

<u>Schütz Oszkár</u> (2022). **Előzetes genetikai eredmények a Kárpát-medencei szarmatákról.** In: XXI. Genetikai Műhelyek Magyarországon Konferencia. Szeged, Hungary (oral presentation)

<u>Schütz Oszkár</u> (2022). **Honfoglalók teljes genomszintű vizsgálata. X. Eötvözet Konferencia.** Szeged, Hungary (oral presentation)

<u>Schütz Oszkár</u> (2022). **Honfoglalók teljes genomszintű vizsgálata. In: VII. Illyés Multidiszciplináris Konferencián.** Budapest, Hungary (oral presentation)

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VIII. Co-Author Declaration

As the first author of the following journal article:

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I hereby declare that the doctoral candidate, Oszkár Schütz contributed significantly to this work. Furthermore, I verify that all the findings/results presented in the article have not been previously used to obtain any PhD degree and will not be used for such purposes in the future.

Szeged, 2025.07.21.	
	Dr. Zoltán Maróti