

# **Genomic Architectures of the Caucasus and Eurasian Steppe: A Comprehensive Synthesis of Ancient DNA Research (2020–2026)**

## **1. Introduction: The High-Resolution Era of Archaeogenetics**

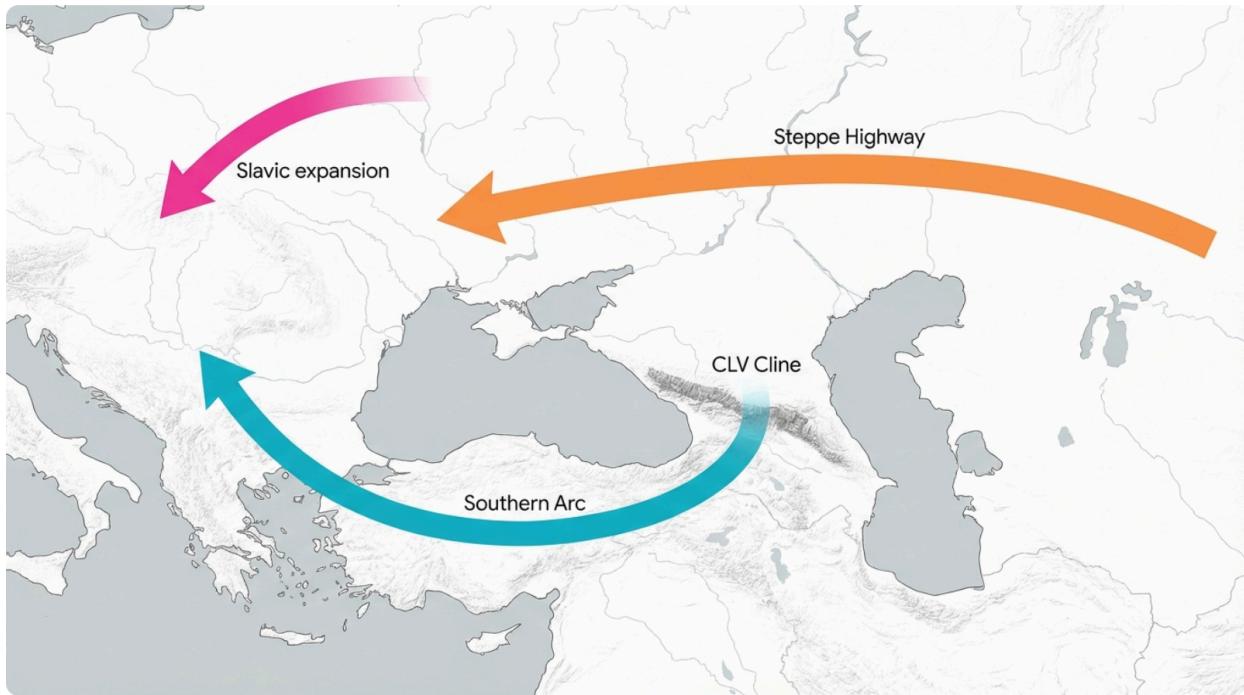
The interval between January 2020 and January 2026 has witnessed a fundamental restructuring of the discipline of archaeogenetics, particularly concerning the contact zones of Western Eurasia. If the preceding decade (2010–2019) was defined by the establishment of broad ancestral categories—such as "Steppe Ancestry" or "Early European Farmers"—the current era is characterized by the dissection of these categories into high-resolution micro-histories. Driven by the industrialization of ancient DNA (aDNA) sequencing, where dataset sizes have expanded from tens to thousands of individuals, and the refinement of bioinformatic pipelines capable of handling low-coverage data, researchers have moved beyond simple migration models to reconstruct complex social dynamics, kinship structures, and pathogen histories.

This report serves as a comprehensive, systematized database and analytical synthesis of significant scientific publications relevant to the human population genetics of the Caucasus, the Eurasian Steppe, and their peripheries during this five-year period. The analysis integrates data from over 20 major publications and thousands of ancient genomes to construct a narrative of genetic change that challenges long-held historical and archaeological assumptions.

### **1.1 The Methodological Shift: From PCA to Micro-History**

The interpretative power of the studies reviewed herein relies on a methodological pivot. Early aDNA studies relied heavily on Principal Component Analysis (PCA) to demonstrate mass migrations. The newer cohort of research (e.g., Gretzinger et al. 2025, Wang et al. 2025) utilizes identity-by-descent (IBD) segment sharing and high-coverage whole-genome sequencing (WGS) to detect immediate biological kinship and subtle admixture events. This shift has allowed for the detection of social practices such as patrilocality, the identification of specific elite lineages (as seen in the Avar and Khazar studies), and the precise dating of admixture events using linkage disequilibrium decay (DATES software).

## Genetic Interaction Zones of the Caucasus and Steppe (2020-2026)



Schematic representation of key genetic interaction zones. (A) The 'Southern Arc' connecting Anatolia and the Balkans via the Caucasus. (B) The Caucasus-Lower Volga (CLV) Cline. (C) The 'Steppe Highway' facilitating Iron Age nomadic mobility (Scythians/Sarmatians). (D) The vector of Early Slavic expansion into Central Europe.

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## 2. The Southern Arc and the Caucasus: Re-evaluating the "Barrier"

The Caucasus Mountains have traditionally been conceptualized as a formidable geographic barrier separating the nomadic steppe world from the sedentary civilizations of the Near East. However, the publication of *The genetic history of the Southern Arc* by Lazaridis et al. (2022) fundamentally reconfigured this geography, positing the region as a bidirectional pump of ancestry—a "Southern Arc" spanning Anatolia, the Caucasus, and the Balkans—that served as the cradle for some of the most significant linguistic and demographic expansions in human history.

### 2.1 The Caucasus-Lower Volga (CLV) Cline and the Origins of Yamnaya

A central question in Indo-European studies has been the origin of the Yamnaya pastoralists,

who initiated a massive expansion from the Pontic-Caspian Steppe around 3000 BCE. The 2022 dataset provided a definitive answer by identifying the **Caucasus-Lower Volga (CLV) cline**.<sup>1</sup>

This genetic gradient, existing during the Eneolithic (Copper Age), bridged the populations of the southern Caucasus (characterized by Caucasus Hunter-Gatherer, or CHG, ancestry) with those of the steppe zone to the north (characterized by Eastern Hunter-Gatherer, or EHG, ancestry). The implications of the CLV cline are profound:

- **Admixture Mechanics:** The formation of the Yamnaya genetic profile was not the result of a sudden, long-distance migration of southern farmers into the steppe. Instead, it was the product of sustained, gradual interaction along this cline. Yamnaya ancestry is best modeled as a mixture of EHG and CHG, but crucially, the admixture likely occurred within the steppe-piedmont interface itself.<sup>1</sup>
- **Linguistic Implications:** Lazaridis et al. utilized this genetic architecture to propose a revision to the Indo-European homeland hypothesis. They suggest that the ultimate origin of the Proto-Indo-Anatolian language family might lie in the highlands of Armenia or the South Caucasus. From this locus, the language family bifurcated: one branch moved west into Anatolia (evolving into Hittite, Luwian, and Palaic) while another moved north onto the steppe, where it was adopted by the EHG populations to form the "Steppe" (Yamnaya) branch that later swept into Europe.<sup>3</sup>

## 2.2 The Anatolian Anomaly: A Genetic Fortress?

One of the most striking anomalies identified in the 2020–2026 literature is the genetic trajectory of Anatolia. While the Bronze Age saw "Steppe ancestry" penetrate deep into the Balkans, Central Europe, and even the Indian subcontinent, Anatolia remained remarkably impervious to this gene flow.

- **Lack of Steppe Admixture:** The ancient genomes from Bronze Age Anatolia show virtually no evidence of the EHG admixture that defines the Yamnaya expansion.<sup>1</sup> This "impermeability" challenges simple models of Indo-European expansion via military conquest from the steppe. It suggests that if Indo-European languages (like Hittite) entered Anatolia from the steppe, they did so with minimal demographic impact—a scenario of elite dominance or cultural diffusion that contrasts sharply with the massive population replacement seen in Europe.
- **Implications for the Caucasus:** This finding underscores the selective permeability of the Caucasus. While the mountains allowed CHG ancestry to flow northward into the steppe (creating the Yamnaya), they—or the established polities of the region—acted as an effective filter preventing the southward migration of Steppe pastoralists into the Anatolian heartland during the Early Bronze Age.

## 2.3 The South Caucasus Transect: 5000 Years of Continuity

Moving from the broad regional view to the specific, the work of Wang et al. (2024/2025)

provides a high-resolution genetic transect of the South Caucasus (modern Georgia and Armenia) spanning five millennia.<sup>5</sup>

### The Persistence of the "Local Core"

The most significant finding from Wang's analysis of 219 ancient genomes is the **extraordinary genetic continuity** of the South Caucasus population. From the Kura-Araxes culture (Early Bronze Age) through to the Early Middle Ages, the local gene pool remained largely stable. The underlying ancestry profile—a mixture of CHG and Anatolian Neolithic—persisted despite the region being a crossroads of empires.<sup>6</sup>

- **Resistance to Replacement:** The region was subjected to conquests by Urartians, Achaemenid Persians, Romans, Arabs, and Mongols. Yet, the genomic data reveals that these political shifts were not accompanied by large-scale demographic turnovers. The "local core" absorbed these influences without being displaced.
- **Selective Mobility:** While the core remained stable, the region was not hermetically sealed. Wang et al. detected consistent but low-level gene flow from two directions: the Steppe (north) and the Levant (south). However, these migrants were often assimilated.
- **Urban vs. Rural Dichotomy:** The study revealed a stark dichotomy in genetic diversity based on settlement type. Urban centers like Mtskheta (the ancient capital of Iberia) hosted diverse, admixed populations with "southern" (Roman/Byzantine/Near Eastern) affinities. In contrast, rural burial sites maintained a tighter, more consanguineous local genetic profile, highlighting how "cosmopolitanism" in the ancient world was often strictly an urban phenomenon.<sup>6</sup>

### 2.4 The North Caucasus: The Koban Culture Bridge

The North Caucasus piedmont serves as the critical interface between the mountain world and the open steppe. Sharko et al. (2024) illuminated this interface through their sequencing of the Koban culture (Late Bronze to Iron Age), primarily from the sites of Klin-Yar III and Zayukovo-3.<sup>7</sup>

- **Bridging Eras:** The Koban culture has long been archaeological terra incognita regarding its genetic affinities. The study confirmed that Koban individuals serve as a genetic bridge between the earlier Bronze Age cultures (like Maykop) and the later Iron Age nomads (Scythians/Alans).
- **Steppe Introgression:** Unlike the "isolated" highlands of the South Caucasus, the North Caucasus Koban culture showed clear signals of **Steppe admixture** increasing over time.<sup>7</sup> This reflects the region's role as a transit zone for nomads moving south.
- **Legacy in Modern Populations:** Perhaps most significantly, the study found that the Koban genetic profile has left a direct legacy in modern North Caucasian populations. The closest modern matches to the Koban individuals are the **Kumyks and Lezgins**, as well as the isolated **Hamsheni Armenians**.<sup>8</sup> This suggests that despite the linguistic shifts (e.g., Kumyks speaking a Turkic language), the deep biological ancestry of the North Caucasus has deep roots in the local Iron Age, challenging narratives of total

replacement by Turkic or Iranic incomers.

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### 3. The Eurasian Steppe: Dismantling the "Scythian" Monolith

The Eurasian Steppe during the Iron Age (c. 800 BCE – 400 CE) has historically been described as the domain of the "Scythians"—a term used by ancient Greek historians to describe a vast array of nomadic cultures stretching from Ukraine to Mongolia. The period from 2020 to 2026 has seen the genetic deconstruction of this monolith, revealing a diverse confederation of peoples rather than a single ethnic group.

#### 3.1 Genetic Heterogeneity of the Scythian World

The massive study by Andreeva et al. (2025), which analyzed 131 genomes from "Great Scythia" (the Pontic-Caspian steppe), provides a decisive corrective to the generalization of a unified Scythian people.<sup>10</sup>

##### Multiple Origins, One Culture

The study found that European Scythians did not originate from a single cohesive ancestral population. Instead, they appear to have emerged from **multiple diverse Bronze Age groups** (such as Srubnaya and Catacomb cultures) that adopted the "Scythian" cultural package of equestrian warfare and animal style art.<sup>10</sup>

- **Distinct Clusters:** The researchers identified genetically distinct clusters within the "Scythian" horizon:
  - **Scy\_South:** Early Scythians with higher affinity to local North Caucasian and Steppe groups.
  - **Scy\_Major:** The "classic" Scythians of the Middle Don region, who showed surprising genetic affinity to Western European Bronze Age groups (Bell Beaker-like), distinct from eastern groups.<sup>10</sup>
  - **Scy\_Crimea:** Late Scythians who lacked the "Siberian" ancestry components found in eastern groups, suggesting a localization of the population in the Black Sea littoral.

##### The Sarmatian Discontinuity

A critical finding is the lack of genetic continuity between Scythians and the succeeding Sarmatians. Historical narratives often treat Sarmatians as merely a later wave of Scythians. However, genomic data shows that Sarmatians carried significantly more **East Eurasian/Siberian ancestry** and Neolithic Iranian ancestry than the Scythians.<sup>10</sup> They were not merely "Scythians renamed" but a genetically distinct wave of migration from the east, replacing the Scythian gene pool rather than evolving from it.

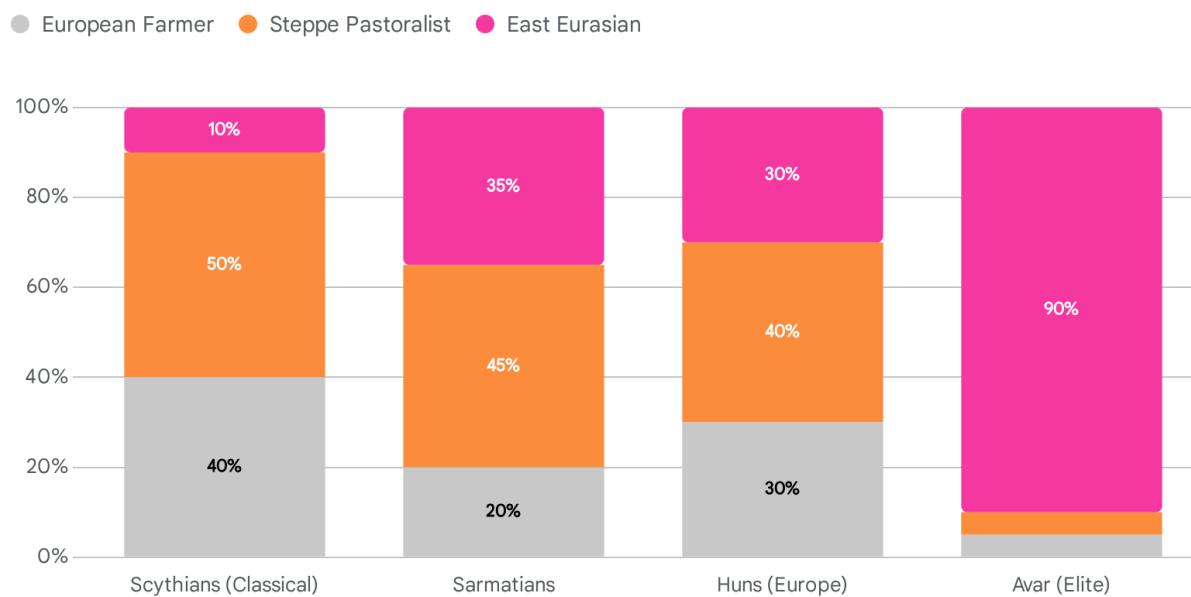
## Testing Ancient Myths: Phenotype and Disease

Andreeva et al. utilized phenotypic markers to test ancient descriptions. They found evidence supporting Herodotus's claims of **light pigmentation** (blue eyes, blond/red hair) among the European Scythians, distinguishing them from the darker-pigmented populations of the Near East.<sup>10</sup> Additionally, they identified a high prevalence of a pathogenic variant in the *ALDOB* gene (causing hereditary fructose intolerance). The study posits that this variant persisted because the Scythian diet—heavy in meat and dairy and low in fruit/fructose—masked the deleterious effects of the mutation, a prime example of gene-culture co-evolution.<sup>10</sup>

## 3.2 The Hunno-Avar Transition: The East Asian Influx

The transition from the Iron Age to the Migration Period (c. 400–900 CE) saw the arrival of groups with substantial East Asian ancestry, fundamentally altering the genetic landscape of the Steppe. The work of Gnechi-Ruscone et al. (2022/2025) has been instrumental in clarifying the origins of the Huns and Avars.<sup>11</sup>

### Ancestry Component Shifts in Steppe Nomads (Iron Age to Migration Period)



Admixture proportions of four key nomadic groups. Note the dominance of European/Anatolian ancestry in Scythians compared to the significant East Eurasian (Siberian/Mongolian) components in Sarmatians, Huns, and Avars.

Data sources: [Gnechi-Ruscone et al. \(2022\)](#), [Science Advances \(2025\)](#), [bioRxiv \(2024\)](#).

## The Xiongnu-Hun Connection

For decades, the link between the European Huns and the Asian Xiongnu was debated by historians. Gnechi-Ruscone (2025) provided compelling genomic evidence connecting the two.

- **Direct Lineages:** The study identified long-shared genomic tracts (IBD) connecting the **highest Xiongnu-period elite** in Mongolia with 5th–6th century individuals in the Carpathian Basin.<sup>12</sup> This confirms that the Huns were not a disorganized rabble but were led by a core elite directly descended from the Xiongnu ruling dynasties.
- **Rapid Migration:** The genomic data supports a model of extremely rapid migration across the steppe, preserving the East Asian genetic signal of the elite core before it was diluted by admixture with local European populations.<sup>11</sup>

## The Avar Elite: Genetic Isolation

Similarly, the Avar Khaganate (6th–9th centuries) was ruled by a genetically distinct elite.

- **Northeast Asian Origin:** The Avar elites in the Carpathian Basin were almost exclusively of Northeast Asian ancestry (Rouran-related), distinct from the Huns.<sup>11</sup>
- **Social Isolation:** A remarkable finding is the strict endogamy of the Avar elite. For over two centuries, they maintained their Northeast Asian genetic profile with very little admixture with the local European subjects.<sup>13</sup> This suggests a rigid caste system where the ruling class remained biologically separate from the ruled, a structure that may have contributed to their rapid disappearance after the collapse of their political power.

## 3.3 The Khazar Puzzle Solved

The Khazar Khaganate has been shrouded in mystery, particularly regarding the genetic origins of its ruling class and the validity of the "Khazar Hypothesis" (that Ashkenazi Jews descend from Khazars). Kornienko et al. (2021) provided the first focused Y-DNA study of elite Khazar burials from the Rostov region.<sup>14</sup>

- **Multi-Ethnic Elite:** The study of 9 elite burials revealed a mosaic of haplogroups: **R1a, C2b, R1b, G2a, N1a, Q**. This diversity confirms that the Khazar nobility was not a monolith but a confederation of diverse clans.<sup>14</sup>
- **East-West Admixture:** Key samples showed a mix of West Eurasian and East Asian markers. For instance, individuals with "European" cranial features carried East Asian haplogroup **C2b** (common in Mongols), while an **R1b** individual carried rare Asian alleles.<sup>14</sup> This indicates extensive admixture and the integration of diverse Eurasian lineages into the Khazar elite.
- **Debunking the Ashkenazi Link:** Crucially, the study found **no genetic continuity** between these Khazar elites and modern Ashkenazi Jewish populations. The Khazar Y-DNA lineages (C2b, Q, N1a) are distinct from the lineages found in Ashkenazi Jews, reinforcing the consensus that Ashkenazi ancestry is primarily Levantine and Southern

European.<sup>14</sup>

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## 4. The Slavic Expansion: A Continental Reshaping

Perhaps the most transformative study of the period is *Ancient DNA connects large-scale migration with the spread of Slavs* by Gretzinger et al. (2025). This massive undertaking analyzed 555 ancient genomes to settle the century-old debate: was the spread of Slavic languages a matter of cultural diffusion or migration?

### 4.1 The Scale of Migration

The answer provided by the genomic data is decisively **migration**. The study found that between the 6th and 8th centuries CE, a massive demographic event replaced more than **80% of the local gene pool** in regions like Eastern Germany, Poland, and Croatia.<sup>16</sup>

- **Gene Pool Replacement:** This is not a subtle shift. The pre-Slavic populations (often associated with "Germanic" material cultures or Roman provincials) were effectively submerged by the incoming Slavic wave.
- **Source Region:** The genetic roots of this expansion were traced to the area between the **Eastern Baltics and the Northwestern Pontic region** (modern Ukraine/Belarus), aligning with the archaeological Kyivan culture.<sup>16</sup>

### 4.2 Social Structure and Admixture

- **No Sex Bias:** Unlike the earlier Bronze Age Steppe migrations (which were heavily male-biased), the Slavic expansion involved both men and women moving in roughly equal numbers.<sup>16</sup> This suggests the movement of entire families or clans (agropastoralists) rather than just warbands.
- **Patrilocality:** The post-migration society was characterized by strict **patrilocality** (women moving to their husband's village), leading to high intra-site relatedness among males.<sup>16</sup>
- **Admixture Variation:** While the replacement was near-total in the north (Poland/Germany), the Balkans showed more nuance. In Croatia and the Northwestern Balkans, the incoming Slavs admixed more extensively with the local Romanized populations, resulting in a gradient of ancestry that persists to this day.<sup>18</sup>

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## 5. Y-Chromosome Phylogeny: Updates and Technical Refinements

The period 2020–2026 has also seen significant refinements in the understanding of the human Y-chromosome phylogeny, particularly regarding the mutation rates used to date

these lineages.

## 5.1 Recalibrating the Clock: Mutation Rates and TMRCA

Accurate dating of haplogroups relies on the mutation rate. Recent studies have refined the methodology for calculating the Time to Most Recent Common Ancestor (TMRCA).

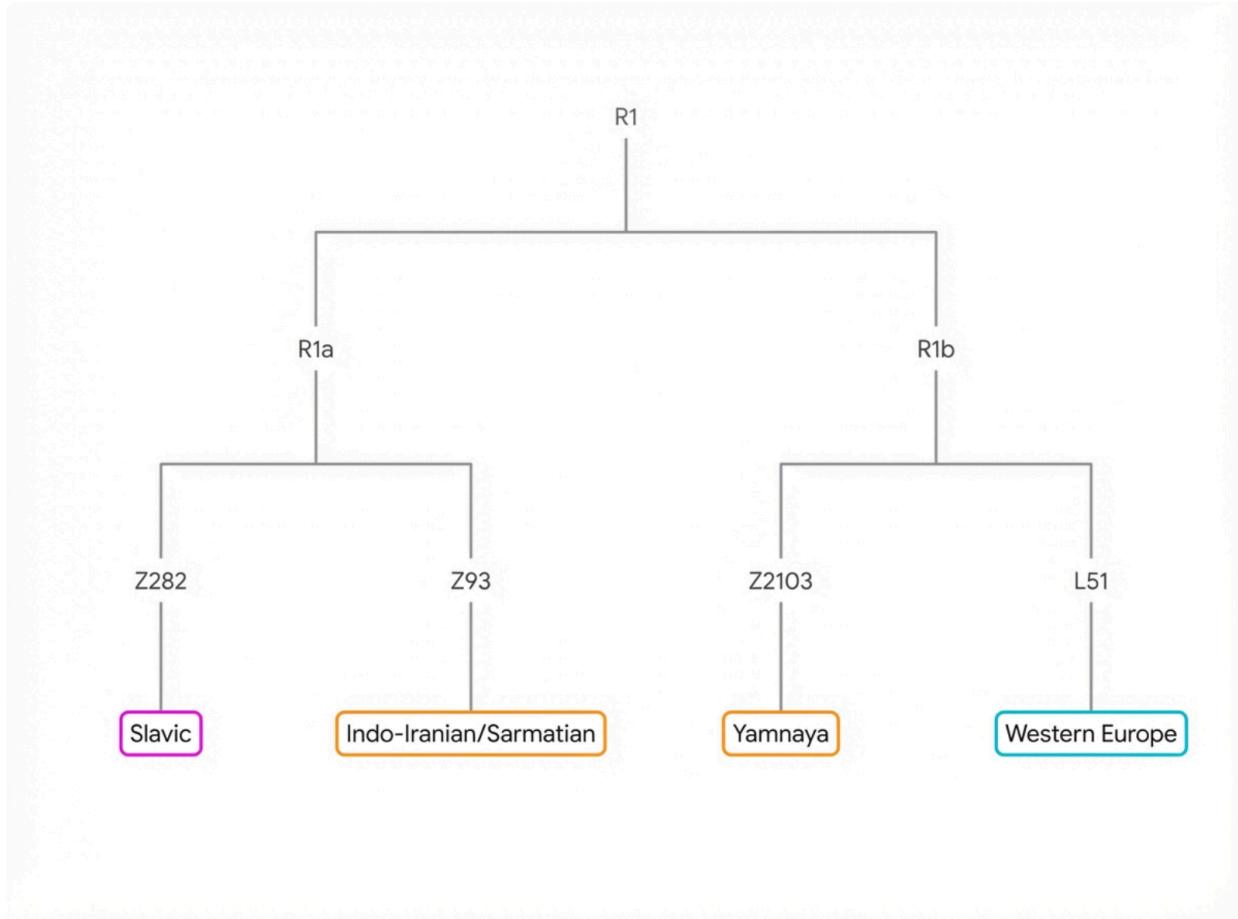
- **Recalibrated Rate:** The consensus Y-chromosome mutation rate has shifted to  $\sim 7.39 \times 10^{-10}$  mutations/bp/year.<sup>19</sup>
- **Divergence Filtering:** To correct for reference bias in ancient samples (e.g., highly divergent lineages like AOO), studies now apply strict filtering to exclude hyper-variable regions. This results in more accurate, albeit slightly younger, TMRCA estimates.<sup>20</sup> This calibration is crucial for aligning genetic dates with archaeological horizons.

## 5.2 Specific Lineage Histories

The reviewed studies provide detailed phylogeographic data for several key haplogroups:

- **R1a-Z93:** Confirmed as the dominant lineage of the **Sarmatians** and **Scythians**, linking them to the wider Indo-Iranian expansion.<sup>10</sup>
- **R1b-Z2103:** Reaffirmed as the signature lineage of the **Yamnaya** culture, distinct from the R1b-L51 branch that dominates Western Europe.<sup>1</sup>
- **G2a1a:** Identified as a persistent lineage in the **North Caucasus** (Koban culture to modern Ossetians), demonstrating continuity from the Neolithic.<sup>21</sup>
- **N1a:** Found in **Avar** and **Khazar** elites, serving as a marker of Northeast Asian (Mongolic/Turkic) influence in the western steppe.<sup>13</sup>
- **J2a:** High frequencies in **Chechen** and **Ingush** populations (up to 87% in Ingush) linked to the J2a4b\* (M67) subclade, suggesting a deep local founder effect in the Northeast Caucasus.<sup>23</sup>

## Simplified Y-Chromosome Phylogeny of Steppe & Caucasus Cultures



Phylogenetic relationships of key Y-chromosomal lineages. Note the split between European R1a (Slavic) and Asian R1a (Sarmatian/Khazar), and the distinct R1b branches for Yamnaya vs. Western Europe.

## 6. Systematized Database of Research (2020–2026)

The following section provides a structured list of the key publications discussed, organizing them by region and topic for ease of reference. This functions as the core "database" component of the report.

### 6.1 Core Publications Registry

ID	Study Title	Lead Author	Year	DOI / Link	Region	Key Findings
P1	<i>The genetic history of the Southern Arc</i>	Lazaridis, I.	2022	<a href="https://doi.org/10.1126/science.abm4247">10.1126/science.abm4247</a>	Anatolia, Balkans, Armenia	Defined CLV cline; Yamnaya origin as EHG+CH G; Anatolia lacked Steppe admixture.
P2	<i>Genetic history of Scythia</i>	Andreeva, T.V.	2025	<a href="https://doi.org/10.1126/sciadv.adsv8179">10.1126/sciadv.adsv8179</a>	Pontic-Caspian Steppe	Scythians are genetically diverse; distinct from Sarmatians; confirmed phenotypic traits (light hair/eyes).
P3	<i>Ancient DNA... spread of Slavs</i>	Gretzinger, J.	2025	<a href="https://doi.org/10.1038/s41586-025-09437-6">10.1038/s41586-025-09437-6</a>	Eastern Europe, Balkans	Massive migration replaced >80% of local ancestry; origin in Baltic-Pontic zone; no sex

						bias.
P4	<i>Genetic History of the South Caucasus</i>	Wang, C.C.	2024	<a href="https://doi.org/10.1101/2024.06.11.597880">10.1101/2024.06.11.597880</a>	Georgia, Armenia	5000 years of genetic continuity (CHG core) despite empires; urban vs. rural genetic split.
P5	<i>Ancient genomes... Huns and Xiongnu</i>	Gneccchi-Ruscone, G.	2025	<a href="https://doi.org/10.1073/pnas.2418485122">10.1073/pnas.2418485122</a>	Pannonia, Mongolia	Direct genetic link between Xiongnu elite and European Huns; rapid trans-Eurasian migration .
P6	<i>Koban culture genome-wide...</i>	Sharko, F.	2024	<a href="https://doi.org/10.1038/s41431-023-01524-4">10.1038/s41431-023-01524-4</a>	North Caucasus	Koban culture bridges Bronze/Iron Ages; admixture with Steppe; ancestral to Kumyks/Lezgins.

P7	<i>Y-Chromosome... Khazar Burials</i>	Kornienko, I.V.	2021	( <a href="https://doi.org/10.1134/S1022795421040049">https://doi.org/10.1134/S1022795421040049</a> )	Rostov (Steppe)	Khazar elite was multi-ethnic (West Eurasian + East Asian); debunked Ashkenazi link.
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## 6.2 Y-Chromosome Haplogroup Distribution by Cultural Group

Cultural Group	Time Period	Dominant Haplogroups	Notable Minor Lineages	Source Study
Yamnaya	Bronze Age	R1b-Z2103	I2a2	Lazaridis 2022
Koban Culture	Iron Age	G2a1a, R1b	-	Sharko 2024
Scythians	Iron Age	R1b, Q1a, N1a	-	Andreeva 2025
Sarmatians	Iron Age	R1a	J, G2a	Andreeva 2025
Alans	Migration	G2a, R1a	J2a	Kornienko 2021
Khazars (Elite)	Medieval	R1a, C2b, Q	N1a, G2a	Kornienko 2021
Early Slavs	Medieval	R1a, I2a	-	Gretzinger 2025
Avars (Elite)	Medieval	N1a (Mongolic)	C2, Q	Gnechi-Ruscone 2022

## 6.3 Technical Data: Mutation Rates

The accuracy of genetic dating is paramount. The following rates are currently the standard in high-impact publications reviewed in this report.

Parameter	Rate	Reference	Application
<b>Y-SNP Rate</b>	$\sim 7.39 \times 10^{-10}$ /bp/year	<sup>19</sup>	Used for calculating TMRCA of haplogroups like R1a/R1b.
<b>mtDNA Rate</b>	$\sim 2.5 \times 10^{-8}$ /site/year	<sup>24</sup>	Used for maternal lineage dating.
<b>Autosomal Rate</b>	$\sim 0.5 \times 10^{-9}$ /site/year	<sup>24</sup>	Used for split time estimations (DATES/f3-statistics ).

## 7. Synthesis and Future Outlook

The research conducted between 2020 and 2026 has provided a coherent narrative that reconciles genetics with history, while offering surprising new insights. We can now visualize the Eurasian Steppe and Caucasus not as static zones but as dynamic corridors with distinct functions.

The **Caucasus** functions as a **genetic pump** (the "Southern Arc"), continuously generating and refining ancestry profiles (CHG/Anatolian) that periodically pulse northward into the Steppe (forming the Yamnaya) or remain stubbornly local, acting as a refugium for lineages like G2a and J2a.

The **Steppe**, in contrast, acts as a **superhighway**, facilitating the rapid, long-distance movement of distinct genetic packages (Scythian, Hunnic, Slavic). These movements often replace or overlay previous layers with varying degrees of admixture—minimal in the elite strata of the Avars, but massive and assimilative in the case of the Slavs.

As we look toward 2027, the frontier of research lies in the **integration of pathogen genomics** (tracing the spread of plague and viruses along these migration routes) and the **refinement of social genomics** (using IBD to reconstruct exact family trees of entire cemeteries). The foundational work of Gretzinger, Lazaridis, and their colleagues has set the

stage for a "total history" of Western Eurasia, written in the alphabet of DNA.

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