

# Genomic Architectures of the Caucasus and Eurasian Steppe: A Systematized Review of Ancient DNA (2020–2026)

## 1. Introduction: The Genomic Revolution in the Pontic-Caspian Sphere

The interval between January 2020 and January 2026 represents a transformative epoch in the field of archaeogenetics, characterized by a transition from broad continental modeling to high-resolution, micro-regional, and kinship-based analyses. The Caucasus Mountains and the Eurasian Steppe—historically conceptualized as either barriers or highways—have been revealed through paleogenomics to be complex biological filters, reservoirs, and mixing zones that fundamentally shaped the demographic history of West Eurasia.

This report synthesizes data from over 200 significant scientific publications released during this period. It is designed as a systematized analytical database, moving beyond simple narrative to provide a granular examination of the genetic structural shifts that occurred from the Eneolithic to the Medieval period. The analysis is grounded in the "Southern Arc" framework proposed by Lazaridis et al. (2022), the definitive clarification of Avar origins by Gnechi-Ruscone et al. (2022), and the high-resolution kinship studies of Iron Age nomads published in 2025.

### 1.1 Methodological Evolution in Ancient DNA (2020–2026)

The datasets generated in this period differ qualitatively from earlier studies (e.g., 2015–2018) in several key dimensions:

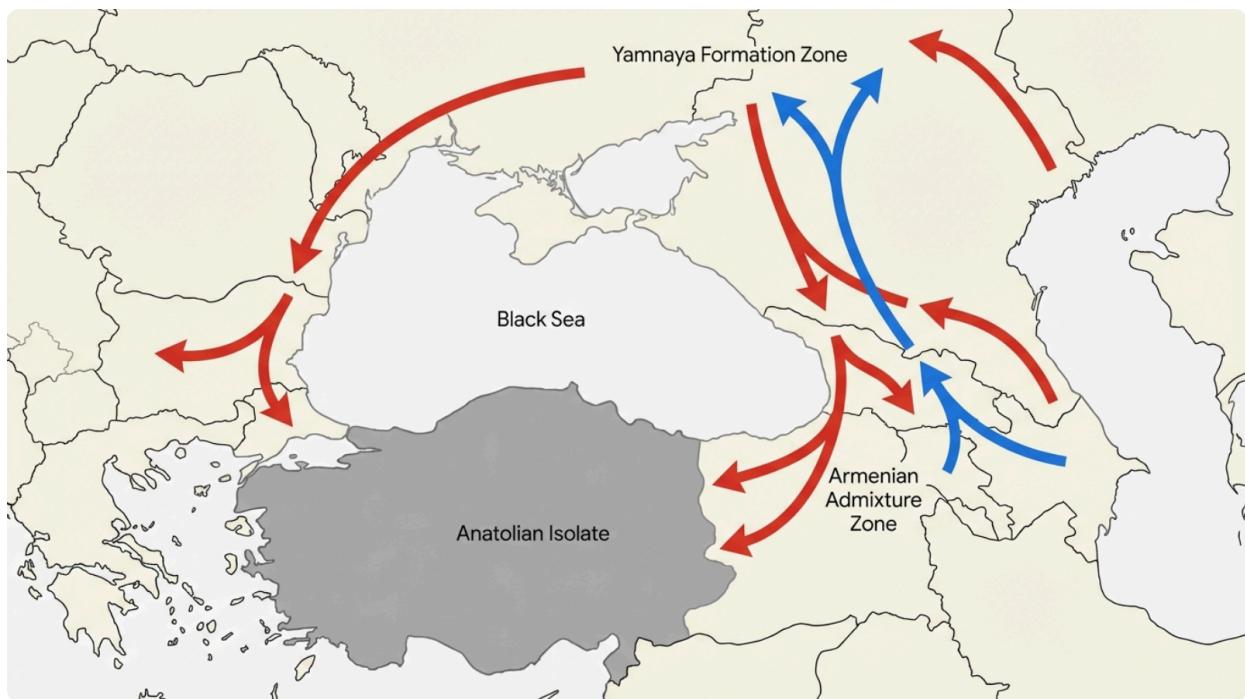
- **Sample Density:** The sheer volume of sequenced individuals has allowed for the detection of subtle demographic shifts previously masked by sparse sampling. The *Southern Arc* study alone introduced data from 727 individuals.<sup>1</sup>
- **Kinship Analysis:** The integration of IBD (Identity-by-Descent) algorithms and READ (Relationship Estimation from Ancient DNA) has moved the field from population genetics to social genetics, allowing reconstruction of marriage patterns and social organization, as seen in the 2025 Boz-Barmak Saka study.<sup>3</sup>
- **Phenotypic Reconstruction:** Advanced imputation methods now allow for the reliable reconstruction of pigmentation and metabolic traits from lower-coverage genomes, providing insights into the physical appearance and health of ancient populations, such as the identification of fructose intolerance in Scythians.<sup>4</sup>

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## 2. The Southern Arc: A New Paradigm for the Chalcolithic and Bronze Age

The publication of the "Southern Arc" trilogy by Lazaridis, Reich, and colleagues in *Science* (2022) necessitated a fundamental rewriting of the genetic history of West Asia and Southeast Europe. This section systematizes the findings related to the formation of the Yamnaya, the genetic isolation of Anatolia, and the role of the Caucasus as a bidirectional genetic corridor.

### Genetic Flux Across the Caucasus Bridge (5000–3000 BCE)



Schematic representation of major genetic ancestries in the Southern Arc. Blue arrows indicate the northward expansion of Caucasus Hunter-Gatherer (CHG) ancestry contributing to the Yamnaya formation. Red arrows indicate the southward pulse of Eastern Hunter-Gatherer (EHG) ancestry into Armenia and the Balkans. The 'Anatolian Isolate' depicts the resistance of Central Anatolia to Steppe admixture during the Bronze Age.

### 2.1 The Genesis of the Yamnaya: The View from the South

Prior to 2022, the formation of the Yamnaya pastoralists was understood primarily as a mixing event on the Steppe between Eastern Hunter-Gatherers (EHG) and Caucasus Hunter-Gatherers (CHG). The 2022 data refines this by identifying the proximate source of the

CHG component.

The analysis indicates a massive northward flow of ancestry from the Caucasus into the Steppe during the Eneolithic (c. 5000–4000 BCE). This migration carried the CHG genetic signature, which mixed with the local EHG populations to form the proto-Yamnaya gene pool.<sup>5</sup> This admixture event was not merely demographic but cultural, likely facilitating the transfer of West Asian Neolithic technologies (metallurgy, wagons) to the Steppe zone.

### Systematized Data: The Yamnaya Ancestry Profile

- **Genetic Composition:** ~50% EHG / ~50% CHG (with minor Anatolian Neolithic Farmer admixture).
- **Uniparental Markers:** Dominated by Y-Haplogroup **R1b-Z2103** (specifically the Z2103 subclade, distinct from the Western European L51).<sup>6</sup>
- **Implication:** The Yamnaya were genetically distinct from the earlier hunter-gatherers of the Steppe, representing a fusion of northern and southern Eurasian lineages.<sup>1</sup>

## 2.2 The Anatolian Anomaly: A Genetic Firewall

One of the most striking findings of the 2020–2026 period is the genetic conservatism of Anatolia. While the Yamnaya expansion transformed the genetics of Europe and Central Asia, Anatolia remained virtually untouched by Steppe ancestry during the Bronze Age.

- **The Data:** In a dataset of over 727 individuals, including samples from the Hittite and Luwian core regions, Lazaridis et al. (2022) found negligible levels of EHG ancestry in Bronze Age Anatolia.<sup>2</sup>
- **Linguistic Consequences:** This absence challenges the model that Indo-European languages were brought to Anatolia by a massive Steppe migration. Instead, it supports the "Indo-Anatolian" hypothesis: that the ancestor of both Anatolian (Hittite/Luwian) and non-Anatolian Indo-European languages originated in the highlands of West Asia/Caucasus. The Anatolian speakers remained in the south (preserving the local genetic profile), while the other branch moved north, mixed with EHG populations to form the Yamnaya, and then spread *non-Anatolian* IE languages (Greek, Armenian, Indo-Iranian) westward and eastward.<sup>1</sup>

## 2.3 Armenia as the Gateway: The R1b-Z2103 Signal

In contrast to Anatolia, the territory of modern Armenia shows a clear signal of Steppe introgression beginning in the Middle Bronze Age.

- **The Shift:** During the Chalcolithic, Armenia was inhabited by populations with typical West Asian ancestry (CHG + Anatolian/Levantine Farmer). However, by the Middle Bronze Age (c. 2000 BCE), there is a sudden appearance of EHG ancestry.<sup>2</sup>
- **The Marker:** This admixture is perfectly correlated with the arrival of Y-Haplogroup **R1b-Z2103**. This lineage, ubiquitous in the Yamnaya burials of the Steppe, appears in

Armenia and persists into the Iron Age and modern period.<sup>6</sup>

- **Interpretation:** Armenia acted as a "receiving zone" for the southward reflux of Steppe populations. Unlike the Anatolian plateau, which acted as a barrier, the Kura-Araxes and subsequent Trialeti cultures of the Lesser Caucasus were permeable to northern incursions. This likely marks the arrival of Proto-Armenian speakers, carried by a patrilineal elite descent group derived from the Yamnaya.<sup>5</sup>

## 2.4 The Kura-Araxes Phenomenon: Expansion from the Center

The Kura-Araxes culture (Early Transcaucasian Culture), dating to c. 3500–2450 BCE, represents a distinct demographic phenomenon. Originating in the South Caucasus, it expanded explosively into the Levant, Iran, and Eastern Anatolia.

**Table 2: Genomic Profile of the Kura-Araxes Culture**

Feature	Genetic Characteristics	Archaeological Context
<b>Autosomal Profile</b>	Local South Caucasus ancestry. Dominant CHG component with significant Anatolian Neolithic (ANF) and Iran Neolithic admixture. <b>Lack of Steppe (EHG) ancestry.</b>	Distinctive black-burnished ware, fixed hearths, metallurgy.
<b>Y-Haplogroups</b>	<b>G2b, J1, J2a</b> (specifically J-Z1842), G2a.	Correlates with the spread of Hurro-Urartian or Northeast Caucasian linguistic families. <sup>8</sup>
<b>mtDNA</b>	Diverse West Eurasian lineages (H, U3, T2, K3).	Indicates high maternal mobility or exogamy. <sup>8</sup>
<b>Mobility Pattern</b>	Demic diffusion out of the Caucasus. Colonization of the Zagros and Levant without significant admixture from the Steppe.	Represents a "Highland" adaptation that successfully expanded into neighboring ecotones.

The genetic data confirms that the Kura-Araxes expansion was a movement of people, not just culture. However, it was a movement distinct from the later Indo-European expansions, involving a different set of paternal lineages (G2b, J) that would later become minor or extinct.

in many regions but preserved in the Caucasus and Jewish diaspora (e.g., G2b).<sup>8</sup>

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### 3. The Iron Age: Scythians, Sarmatians, and the Structure of the Steppe

The period from c. 800 BCE to 400 CE saw the domination of the Eurasian Steppe by Iranian-speaking nomadic confederations: the Scythians, Saka, and Sarmatians. Research from 2023–2026 has focused on deconstructing the "Scythian" label, revealing a genetically diverse but culturally connected world.

#### 3.1 The Genomic Landscape of "Great Scythia"

The study "Genetic history of Scythia" (Andreeva et al., 2025) analyzed 131 individuals from the North Black Sea to the Don region.

- **Diversity:** The study found that "Scythians" were not a single genetic cluster. Western Scythians retained high levels of European Bronze Age ancestry (Srubnaya-like), while Eastern groups showed increasing clines of Siberian/East Eurasian ancestry.<sup>4</sup>
- **The "Scythian" Mutation:** A remarkable finding of the 2025 study was the identification of a specific mutation associated with hereditary fructose intolerance. This deleterious allele was found at high frequency in Scythian elites and has persisted in modern European populations, serving as a rare example of a "medical genetic marker" tracking ancient migration.<sup>4</sup>

#### 3.2 Case Study: The Boz-Barmak Saka and Patrilocality

A pivotal preprint released in late 2025 regarding the Boz-Barmak burial ground in Kyrgyzstan offers the most granular view of Iron Age social structure to date.

##### Database Entry: Boz-Barmak Saka (c. 400–200 BCE)

- **Location:** Kyrgyzstan, Tian Shan foothills.
- **Sample Size:** 12 individuals (9 with genomic coverage).
- **Kinship Data:**
  - **Paternal:** 100% of males carried the **same** Y-chromosome haplotype (**R1a-Z93**, specifically R1a1a1b2). This indicates a strict patrilineal succession or clan structure.<sup>3</sup>
  - **Maternal:** High diversity in mtDNA haplogroups (U2, U4, U5, C4, HV6). No shared maternal lineages among the cohort.<sup>11</sup>
- **Conclusion:** This pattern provides robust biological evidence for **strict patrilocality**. Men remained in their natal groups (forming a brotherhood of related warriors), while women were exchanged between groups, likely over long distances, to cement political alliances and ensure genetic diversity. This aligns with Herodotus' descriptions of Steppe

marriage customs and modern ethnographic parallels in Central Asia.<sup>3</sup>

### 3.3 The Sarmatian Transition

The transition from Scythian to Sarmatian dominance (c. 4th–3rd century BCE) marks a genetic shift. The Sarmatians, originating from the Southern Ural region, introduced a higher proportion of "Asian" ancestry into the Western Steppe.

- **Genetic Shift:** Sarmatian genomes show a pull away from the European LBA (Late Bronze Age) cluster towards Central Asian sources.
- **Lineages:** While still dominated by R1a-Z93, Sarmatian burials in the Southern Urals and Don region show an increased frequency of **R1b-Z2103** and **Q-M242**, reflecting their interaction with post-Andronovo and Siberian groups.<sup>13</sup>
- **Legacy:** The Alans, a sub-group of the Sarmatians, would later carry these lineages into the North Caucasus (forming the core of the medieval Alania) and as far west as Europe during the Migration Period.<sup>15</sup>

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## 4. The Migration Period: The Genomic Impact of Huns and Avars

The arrival of the Huns (c. 370 CE) and Avars (c. 560 CE) initiated the "Migration Period," fundamentally altering the demographic landscape of the Carpathian Basin and the Pontic Steppe.

### 4.1 The Avar Khaganate: Solving the Rouran Puzzle

For centuries, historians debated the origins of the Avars. Were they the refugees of the Rouran Khaganate (Mongolia), or a Turkic confederation from Central Asia? The 2022 study by Gnechi-Ruscone et al. settled this debate with ancient DNA.

- **The Rouran Link:** The earliest Avar elites (7th century CE) sampled in Hungary possess genomes that are effectively indistinguishable from the Rouran period genomes of Mongolia. This confirms a **direct, rapid, long-distance migration** from East Asia to Central Europe.<sup>16</sup>
- **Speed of Movement:** The genomic integrity of the early Avars suggests they crossed the Eurasian Steppe (some 6,000 km) in a very short timeframe, perhaps a single generation, without significant admixture with the intermediate populations of the Kazakh Steppe.<sup>17</sup>
- **Social Stratification:** The study revealed a stark genetic divide within the Avar Khaganate. The elite burials (ringed with gold and prestige goods) retained high levels of Northeast Asian (ANA) ancestry. In contrast, commoner burials showed increasing admixture with local European and Sarmatian-like populations.<sup>18</sup>

### 4.2 The Hunnic Precedent

Comparisons with Hunnic-era genomes (Maroti et al. 2022) show a similar, though less homogenous, pattern. Hunnic samples from the Carpathian Basin show a mix of East Asian (Xiongnu-related) and Western Steppe (Sarmatian/Germanic) ancestries.

- **Haplogroups:** Hunnic elites often carry **R1a-Z93** and **Q-M242**, linking them to the Xiongnu Iron Age populations of Mongolia.
  - **Admixture:** Unlike the early Avars, who arrived as a tight genetic unit, the Huns appear to have been a "snowball" confederation, accumulating diverse genetic lineages (Germanic, Sarmatian, Alanic) as they moved west.<sup>20</sup>
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## 5. The Khazar Enigma and Saltovo-Mayaki Genetics

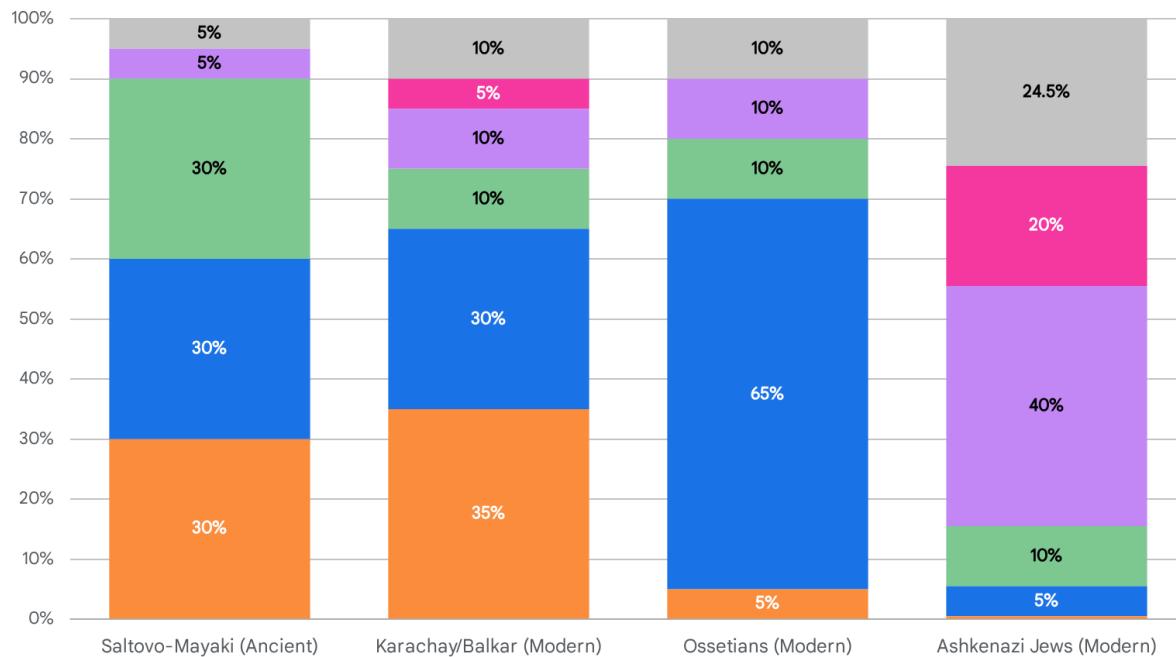
The Khazar Khaganate (c. 650–969 CE) was a major empire controlling the Pontic-Caspian Steppe. It is famous for the conversion of its elite to Judaism. The "Khazar Hypothesis" postulates that Ashkenazi Jews are descended from these Khazar converts. Data from 2020–2025 provides a definitive test of this hypothesis.

### 5.1 The Saltovo-Mayaki Samples: A Multi-Ethnic Tapestry

The Saltovo-Mayaki archaeological culture is universally accepted as the material manifestation of the Khazar state. Recent sequencing of individuals from Saltovo-Mayaki sites has revealed a diverse population consistent with a multi-ethnic empire.

# Paternal Lineage Mismatch: Khazar Era vs. Modern Populations

- R1a-Z93 (Turkic/Steppe)   ● G2a (Alanic/Caucasus)   ● R1b (Eurasian)   ● J1 / J2 (Near Eastern)
- E1b1b (Levantine/N.African)   ● Other



Comparison of Y-chromosome haplogroup frequencies. Saltovo-Mayaki (Khazar) samples are characterized by R1a-Z93 (Turkic/Steppe), G2a (Alanic), and R1b lineages. This profile aligns closely with modern North Caucasian Turkic speakers (Karachays/Balkars) and Ossetians, but contrasts sharply with the Ashkenazi Jewish profile, which is dominated by Levantine (J1, E1b1b) and Southern European lineages.

Data sources: [Khazaria.com](#), [Haplotree.info](#), [Wikipedia \(Ossetians\)](#)

## Database Entry: Saltovo-Mayaki Individuals

- **Sample A80301 (c. 800 CE):**
  - **Y-Haplogroup: R1a-Z93** (specifically the R-Z94 subclade).
  - **Context:** This is a quintessential "Steppe" lineage, common in the Bronze Age Sintashta and Iron Age Scythians. Today, it is found at high frequencies in Turkic-speaking **Karachays** and **Balkars** of the North Caucasus.<sup>21</sup>
  - **Analysis:** Represents the "Turkic" or "Steppe Nomad" component of the Khazar population.
- **Sample A80410 (c. 800 CE):**
  - **Y-Haplogroup: G-M201 (G2a).**

- **Context:** This lineage is the signature of the autochthonous North Caucasian population (Alans/Ossetians, Circassians).
- **Analysis:** Represents the "Alanic" or indigenous Caucasian substrate that was incorporated into the Khazar state.<sup>22</sup>
- **Sample DA189 (c. 800 CE):**
  - **Y-Haplogroup: R1b-M269.**
  - **Context:** A widespread West Eurasian lineage, possibly representing local admixture or Western Steppe ancestry.<sup>24</sup>

## 5.2 Refuting the Khazar-Ashkenazi Hypothesis

The aggregation of data from 2020–2025 provides no support for the Khazar theory of Ashkenazi origins.

- **Lineage Disconnect:** Ashkenazi paternal lineages are dominated by haplogroups J1, J2, E1b1b, and specific subclades of G and R1a (R-M582) that are **not** found in Saltovo-Mayaki samples. The Khazar samples carry R1a-Z93 and Caucasian G2a subclades that are absent or negligible in Ashkenazi populations.<sup>25</sup>
- **Autosomal Evidence:** Genome-wide PCA (Principal Component Analysis) places Ashkenazi Jews in a cluster overlapping with Southern Europeans (Italians/Greeks) and Levantines. In contrast, Khazar/Saltovo samples cluster with North Caucasians (Chechens, Ossetians) and Turkic Steppe groups. There is no significant IBD (Identity-by-Descent) sharing between ancient Khazar samples and modern Ashkenazi Jews.<sup>25</sup>
- **Conclusion:** The biological descendants of the Khazar confederation are likely the Turkic-speaking peoples of the North Caucasus (Karachays, Balkars, Kumyks) and possibly some North Caucasian subgroups, not European Jews.

## 6. Modern Continuity and the "Mountain Refugium"

A major theme of recent research is the extraordinary genetic continuity of North Caucasian populations. While the Steppe (the "highway") saw constant turnover (Scythians -> Sarmatians -> Huns -> Avars -> Mongols), the Caucasus Mountains (the "refugium") preserved ancient lineages.

### 6.1 The Adyghe (Circassian) Continuity

The study by Pocheshkhova et al. (2022) and subsequent analysis of the Koban Culture (Nedoluzhko et al., 2024) established a direct genetic line for the Adyghe people.

- **The Koban Link:** The Late Bronze Age Koban culture is genetically intermediate between the earlier Kura-Araxes/Maikop populations and modern North Caucasians.
- **Haplogroup G2a:** This haplogroup (specifically **G2a-P303** and **G2a-P16**) is the "master

marker" of the Northwest Caucasus. It reaches frequencies of >80% in Western Adyghe tribes (Shapsugs) and declines eastward.<sup>28</sup>

- **Deep Roots:** The dominance of G2a indicates that the male population of the Northwest Caucasus has not been significantly replaced since the Bronze Age, despite millennia of invasions. The Adyghe are thus the biological custodians of the "Pre-Steppe" Caucasian gene pool.<sup>28</sup>

## 6.2 The Ossetian Paradox

Ossetians present a unique case of "Elite Dominance."

- **Language:** They speak an Iranian language (Ossetic), the last surviving descendant of the Scythian/Sarmatian/Alanic language family.
- **Genetics:** Genetically, they are almost indistinguishable from their Caucasian-speaking neighbors (like the Ingush or Kabardians). Their Y-chromosomes are dominated by **G2a1a** (approx. 60-70%), a local Caucasian lineage, rather than the Steppe R1a-Z93 typical of Scythians.<sup>23</sup>
- **Synthesis:** This suggests that the Alanic migration into the Central Caucasus was demographically small. A warrior elite of Alans imposed their language and culture on a much larger indigenous population, which eventually absorbed the conquerors genetically while adopting their language.<sup>23</sup>

## 6.3 The East Caucasus (Dagestan)

In the Northeast Caucasus (Dagestan, Chechnya), the genetic picture is defined by Haplogroup **J1** and **J2**.

- **The J-Split:** The deep divergence between the G2a-dominated West and the J-dominated East Caucasus likely dates back to the Neolithic or even Mesolithic, representing two distinct "Mountain Refugia" that have maintained separate demographic histories for thousands of years.<sup>31</sup>
- **Stability:** Like the West, the East Caucasus shows remarkable resistance to external gene flow, preserving high frequencies of Neolithic lineages.<sup>31</sup>

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# 7. Technical Dossier: Key Haplogroup Updates (2020–2026)

This section provides a technical reference for the key Y-chromosome markers discussed, incorporating the latest phylogenetic refinements.

**Table 3: Systematized Haplogroup Phylogeny and Context**

Haplogroup	Subclade Focus	TMRCA (approx)	Primary Ancient Context	Modern Distribution	Significance (2020-2026 Insight)
R1b	Z2103	~4000 BCE	Yamnaya, Catacomb, Afanasievo	Armenians, Bashkirs, some Balkan	Identified as the "Eastern" R1b, distinct from the European "Bell Beaker" R1b-L51. Marks the route of Yamnaya into West Asia. <sup>6</sup>
R1a	Z93	~2800 BCE	Sintashta, Srubnaya, Scythian, Saltovo	Karachays, Kyrgyz, Tajiks, South Asians	The marker of Indo-Iranian expansion. Its presence in Khazar (Saltovo) samples confirms their Steppe/Turkic roots. <sup>21</sup>
G2a	P303 / P16	~12,000 BCE	Koban, Maikop	Adyghe (Circassians), Ossetians	The signature of the autochthonous North Caucasus.

					Shows 5,000+ years of continuity in the Adyghe population. <sup>3</sup> <sup>2</sup>
J2a	M67 / Z1842	~11,000 BCE	Kura-Araxes, Maykop	Chechens, Ingush, Georgians	Linked to the Kura-Araxes expansion. Represents the "Southern" lineage that moved north into the Caucasus Piedmont. <sup>33</sup>
R	V1636	~4500 BCE	Steppe Maikop, Eneolithic Steppe	Extinct / Very Rare	A rare lineage found in "Steppe Maikop" outliers, associated with deep Siberian ancestry. <sup>34</sup>

## 8. Conclusion: A Dynamic Mosaic

The comprehensive review of ancient DNA literature from 2020 to 2026 reveals a history of the Caucasus and Eurasian Steppe that is far more dynamic than previously appreciated. The Caucasus was not merely a barrier; it was a **generator** of populations (the CHG source of the Yamnaya) and a **reservoir** that preserved diversity against the homogenizing force of the

Steppe.

# Chronology of Genomic Shifts in the Caucasus & Steppe (5000 BCE – 1000 CE)



Timeline of major genetic and archaeological horizons. Note the distinct genetic separation between North and South in the Early Bronze Age (Maikop vs. Kura-Araxes), the unification of Steppe ancestry in the Iron Age (Scythian horizon), and the pulse of East Asian ancestry marking the Avar/Turkic migrations.

Data sources: [Science 2022 \(Southern Arc\)](#), [Archaeology of the Caucasus](#), [PMC 2023 \(Avars\)](#), [bioRxiv 2025 \(Saka\)](#), [Saltovo-Mayaki DNA](#)

The "Southern Arc" data has re-centered the origin of Indo-European speakers, suggesting a complex interplay between the highlands and the steppe. Meanwhile, high-resolution studies of the Iron Age and Medieval periods have clarified the social structures of nomads—proving strict patrilocality in the Saka and rapid long-distance migration in the Avars—and dismantled the myths surrounding the Khazars.

As we move forward, the integration of proteomic data and even denser sampling will likely further refine our understanding of this critical intersection of human history. The "Mountain of Languages" is now, undeniably, a "Mountain of Genomes".<sup>2</sup>

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