

The Genomic Landscape of the Caucasus: A Decade of Ancient DNA Research (2015–2025)

1. Introduction: The Genetic Archive of the Caucasus

The Caucasus region, a formidable mountainous isthmus situated between the Black and Caspian Seas, has long been recognized by historians, archaeologists, and linguists as a pivotal corridor for human migration and a crucible of cultural innovation. For millennia, it has served as both a bridge connecting the Eurasian Steppe to the Near East and a barrier fostering deep genetic and linguistic substructure. The period from 2015 to 2025 marked a revolutionary epoch in the study of this region's prehistory, driven by the explosive maturation of paleogenomics. This report provides a comprehensive synthesis of ancient DNA (aDNA) research conducted over this decade, integrating data from landmark studies including Wang *et al.* (2019), Lazaridis *et al.* (2022), Harney *et al.* (2024), and the recent extensive work on Scythians by Andreeva *et al.* (2025).

The primary objective of this report is to compile and analyze a "virtual database" of genomic data from the Caucasus, encompassing the Mesolithic through the medieval period. By synthesizing genome-wide SNP data, uniparental markers (Y-chromosome and mitochondrial DNA), and archaeological context, we aim to reconstruct the demographic history of the region. This analysis moves beyond simple descriptive statistics to explore second-order insights regarding social organization, patrilocality, the spread of Indo-European and Caucasian languages, and the persistence of specific genetic lineages in modern populations.

From the discovery of the distinct "Caucasus Hunter-Gatherer" (CHG) ancestry component to the complex interactions of the "Southern Arc," the genetic record reveals a history defined by punctuated equilibrium—long periods of regional stability interrupted by profound demographic shifts associated with the Maykop, Yamnaya, Kura-Araxes, and Scythian expansions. This report details these transitions, offering a granular look at the specific samples and cultures that have redefined our understanding of West Eurasian prehistory.

The geographic interactions analyzed in this report span a vast temporal range, from the Mesolithic to the Medieval period. The data reveals distinct "spheres of influence" where genetic components flowed in specific directions. For instance, the Early Bronze Age saw a northward expansion of Near Eastern lineages associated with the Kura-Araxes and Maykop cultures, effectively colonizing the mountain corridor. Conversely, the Middle to Late Bronze Age and subsequent Iron Age were characterized by a southward counter-flow of Steppe ancestry (EHG) into the Southern Caucasus, a movement often correlated with the spread of Indo-European languages. These bidirectional flows underscore the Caucasus not merely as a

barrier, but as a permeable membrane that selectively filtered human migration.

2. The Substratum: Paleolithic and Mesolithic Foundations

The genetic history of the region is anchored by the definition of the **Caucasus Hunter-Gatherer (CHG)** ancestry. This component, first identified in samples from western Georgia, represents a lineage that diverged from Early European Farmers and Western Hunter-Gatherers roughly 25,000 years ago, evolving in isolation within the mountain refuge during the Last Glacial Maximum (LGM).

2.1 The Deep Roots: Satsurblia and Kotias

The definition of the CHG component rests primarily on two high-coverage genomes from Western Georgia, which have become the standard reference points for all subsequent admixture modeling in West Eurasia.

- **SATP (Satsurblia Cave, Georgia):** Dated to approximately 13,000 BP (Upper Paleolithic). This individual represents the deep ancestral root of the CHG component. Crucially, the Y-chromosome analysis identified haplogroup **J1-FT34521** (a branch of J1*), while the mitochondrial lineage was assigned to **K3**.¹ The genomic isolation of this individual suggests that during the LGM, the Southern Caucasus functioned as a refugium, separated from the populations of the Levantine corridor and the Anatolian plateau.
- **KK1 (Kotias Klde, Georgia):** Dated to roughly 9,700 BP (Mesolithic). This individual, living nearly three millennia after the Satsurblia hunter, shows strong genetic continuity with the earlier inhabitant, demonstrating the stability of the CHG population structure over thousands of years. The Y-haplogroup **J2a (J-Y12379)*** and mtDNA **H13c** found in KK1 link these Mesolithic foragers to lineages that are still prevalent in the region today.¹

Recent analyses have pushed this timeline back even further. Samples from **Dzudzuana Cave** (dated to ~26,000 BP) suggest an affinity to both later CHG populations and Villabruna-related clusters, implying that the genetic differentiation between the "Southern" (Caucasus/Near East) and "Northern" (EHG/WHG) Eurasian lineages was a complex, gradual process involving pulses of admixture even before the Holocene.²

Insight: The dominance of Y-haplogroup **J** (both J1 and J2 branches) in these earliest samples establishes a strong signal of patrilineal continuity in the Southern Caucasus. Unlike Western Europe, where Mesolithic haplogroups (like I2) were largely replaced by Neolithic immigrant lineages (G2a), the Southern Caucasus shows a persistence of local J lineages that were eventually incorporated into later Neolithic and Bronze Age expansions. This separation between the CHG populations and the **Eastern Hunter-Gatherers (EHG)** of the northern steppes (characterized by R1a/R1b lineages) creates the fundamental "north-south" genetic

dichotomy that defines the region's subsequent history.

3. The Eneolithic Transition (c. 5000 – 4000 BCE)

The Eneolithic period witnesses the first major interactions between the distinct zones. We observe a genetic boundary in the North Caucasus piedmont: populations in the foothills show a mixture of EHG and CHG, foreshadowing the formation of the Yamnaya genotype, while groups further south remain predominantly CHG/Anatolian-like.

3.1 The Eneolithic Steppe Cline

Samples from the **Progress-2** and **Vonyuchka-1** sites in the North Caucasus piedmont (dated to ~4300 BCE) have provided critical evidence for the formation of the "Steppe" ancestry profile. Unlike the later Yamnaya, who had significant Anatolian Farmer ancestry, these Eneolithic individuals model as a mixture of EHG and CHG without the farmer input. This suggests they represent a "proto-Yamnaya" population formed by the mating of northern hunter-gatherers with CHG groups pushing north through the mountains.⁴

3.2 The Darkvetsi-Meshoko Complex

In contrast to the admixture seen in the steppe piedmont, the **Darkvetsi-Meshoko** culture in the Northwest Caucasus shows a closer affinity to the south. Genetic analysis reveals these individuals carried CHG and Anatolian Neolithic ancestry, suggesting they were part of a northward expansion of the farming lifestyle across the mountains. This cultural complex likely laid the demographic foundations for the subsequent Maykop culture, establishing a sedentary, farming-based population distinct from the mobile foragers and proto-pastoralists of the steppe.

4. The Early Bronze Age: Maykop and Kura-Araxes (c. 4000 – 2500 BCE)

This era is defined by two massive cultural complexes: the **Maykop** culture in the North Caucasus and the **Kura-Araxes** (Early Transcaucasian) culture in the South. Both represent sophisticated societies with advanced metallurgy, yet their genetic stories are markedly different.

4.1 The Maykop Phenomenon: Dual Origins

The Wang *et al.* (2019) study was pivotal in resolving the origins of the Maykop culture, revealing it was not a monolithic entity but rather composed of two genetically distinct populations that shared a material culture.

Maykop Proper (Sedentary/Piedmont)

The individuals associated with the classic rich kurgan burials of the Maykop culture (e.g., sample **OS5002**) are genetically "southern." They model as a mixture of CHG and Anatolian Neolithic ancestry, with minimal to no contribution from the EHG populations of the steppe. This genomic profile is virtually indistinguishable from contemporary populations in Western Georgia, confirming that the rise of Maykop involved a massive northward migration of people who colonized the fertile river valleys of the North Caucasus.⁴

Steppe Maykop (Nomadic/Steppe)

In the arid steppe lands north of the Kuban and Terek rivers, archaeologists identified sites with Maykop-style pottery but distinct burial traditions. Wang *et al.* (2019) labeled this the "Steppe Maykop" cluster. Genetically, these individuals (e.g., **SA6013**, **AY2003**) are radically different from the Maykop Proper. They harbor substantial EHG ancestry and, most surprisingly, a unique **Siberian/Native American-related component** linked to Upper Paleolithic Siberians (like Afontova Gora).⁴

- **Y-DNA Findings:** The paternal lineages of Steppe Maykop emphasize this distinction. While Maykop Proper males often carry **G2a** or **J** lineages, Steppe Maykop males carry lineages like **Q1a** and **R1a**. Specifically, sample **SA6013** carried Y-haplogroup **R-YP1272**, a rare, archaic branch of R1a that is distinct from the R1a-M417 branch that would later dominate the Indo-European expansions.⁶
- **Implications:** The existence of Steppe Maykop proves that the cultural influence of Maykop extended into the steppe through exchange rather than demic diffusion. It also documents a previously unknown migration of Siberian-related peoples into the North Caucasus steppe in the 4th millennium BCE, a lineage that largely disappears in later periods.

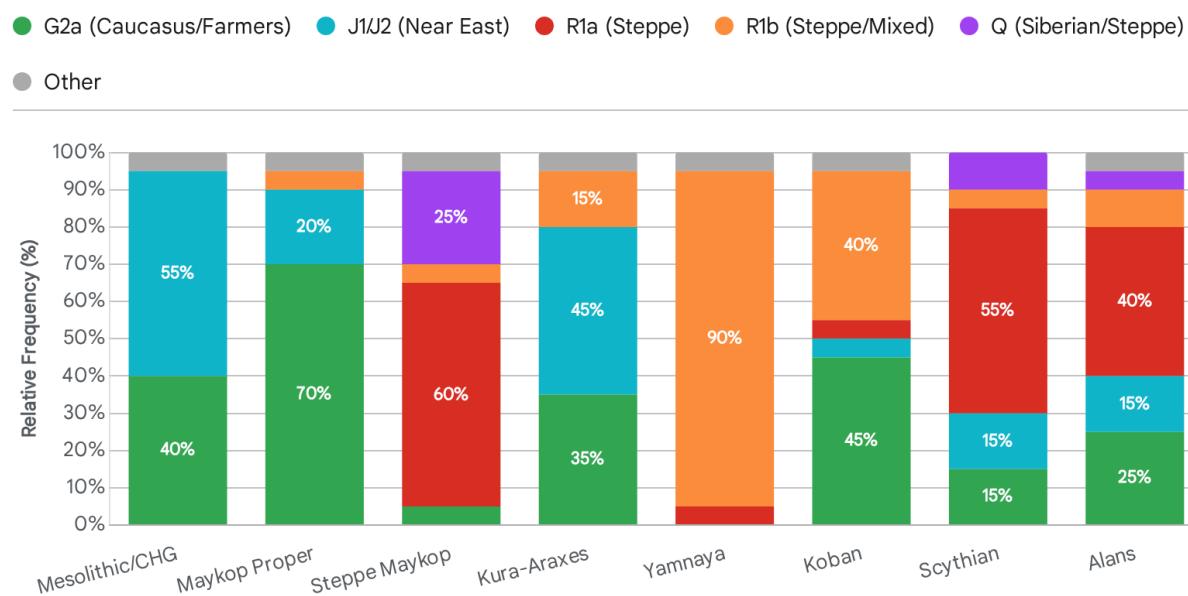
4.2 The Kura-Araxes Expansion

Simultaneous with Maykop, the **Kura-Araxes** culture expanded from the Southern Caucasus to cover a vast area extending from the Northeast Caucasus (Dagestan) to the Levant and Iran.

- **Genetic Homogeneity:** The Kura-Araxes samples analyzed by Lazaridis *et al.* (2022) and others show a remarkable genetic homogeneity across this vast territory. They can be modeled as a mixture of local CHG, Anatolian Neolithic (ANF), and Iranian Neolithic ancestries.⁸
- **Key Samples:**
 - **ARM002 (Kaps, Armenia):** Dated to the Early Bronze Age (3356–3102 BCE). This individual carried Y-Haplogroup **G2b (G-Z8024)** and mtDNA **K3**, linking the culture to deep Iranian/Caucasus paternal lineages.¹⁰
 - **VEK007 (Velikent, Dagestan):** Dated to ~3000 BCE. This sample demonstrates the northward extent of the Kura-Araxes genetic profile into the coastal Caspian plain, confirming the archaeological theory of a "Kura-Araxes wedge" moving north along the coast.¹²

- **Patrilocality and Male Lineages:** The culture is overwhelmingly associated with haplogroups **G2a** and **J2**. The consistency of these paternal markers across geographically distant Kura-Araxes sites suggests a strong system of patrilocality and perhaps a patrilineal clan structure that facilitated their expansion. The absence of Steppe-associated R1a or R1b lineages in the Kura-Araxes core zone (Armenia) until the very end of the period is a critical finding, suggesting the Caucasus mountains acted as an effective barrier to Steppe gene flow during the Early Bronze Age.⁹

Paternal Lineage Composition by Archaeological Culture (4500 BCE - 500 CE)



Distribution of Y-chromosome haplogroups across major archaeological cultures in the Caucasus and adjacent Steppe. The 'Steppe' cultures (Yamnaya, Steppe Maykop, Scythian) are dominated by R-lineages (R1a, R1b) and Q, while the 'Mountain/South' cultures (Kura-Araxes, Maykop, CHG) are characterized by G, J1, and J2 lineages. The Koban culture exhibits a mixed profile, reflecting its position as a cultural bridge.

Data sources: [Wang et al. \(2019\)](#), [Opera Med Phys](#), [MDPI \(Genes\)](#), [Wikipedia \(Kura-Araxes\)](#), [PMC \(Koban/Maykop\)](#), [Haplotype \(Ancient DNA\)](#), [DNA Genics](#), [PMC \(Scythian\)](#)

5. Transition Analysis: The Steppe Introgression

The genetic trajectory of the Caucasus is characterized by a major disruption following the Early Bronze Age. This transition is fundamental to understanding the ethnolinguistic

landscape of the region today.

5.1 The Middle Bronze Age Shift (c. 2500 – 1500 BCE)

Following the collapse of the Kura-Araxes and Maykop phenomena, the genetic barrier of the Caucasus mountains was breached. Lazaridis *et al.* (2022) documented a sharp influx of **Eastern Hunter-Gatherer (EHG)** ancestry into the Southern Caucasus starting in the Middle Bronze Age (MBA). This admixture event coincides with the rise of the **Trialeti-Vanadzor** and later **Lchashen-Metsamor** cultures.

- **The Y-DNA Signal:** The smoking gun for this transition is the appearance of haplogroup **R1b-Z2103**. Completely absent in the thousands of years of Neolithic and EBA history in the Armenian Highlands, this lineage appears suddenly and frequently in MBA and LBA samples. R1b-Z2103 is the signature lineage of the Yamnaya culture from the Pontic Steppe. Its arrival in Armenia and Georgia indicates a direct migration of pastoralist groups from the north, moving through the passes of the Caucasus.¹⁴
- **Linguistic Implications:** This genetic shift is widely hypothesized to correlate with the introduction of **Proto-Armenian** speakers into the region. The admixture profile (Steppe + Local) matches the expected signature for an Indo-European population arriving from the steppe and mixing with local inhabitants. This contrasts with the contemporary Urartian populations, who largely retained the older, local genetic profile without significant Steppe admixture, consistent with their non-Indo-European (Hurro-Urartian) linguistic affiliation.⁸

6. The Iron Age Crucible: Koban, Scythians, and Sarmatians

The Iron Age (c. 1000 BCE – 300 CE) intensified the interaction between the nomadic steppe world and the sedentary mountain populations. The "Bridge" function of the Caucasus became fully operational during this era.

6.1 The Koban Culture: A Genetic Mixing Pot

The **Koban culture** (Late Bronze/Early Iron Age), centered in the North Central Caucasus, represents a critical fusion point. Recent studies by Boulygina *et al.* (2020) and Harney *et al.* (2024) have sequenced individuals from key sites like **Zayukovo-3** and **Klin-Yar III**.

- **Genetic Profile:** Koban individuals display a base of local North Caucasus ancestry (similar to the Bronze Age locals) but with sporadic outliers and clear signs of admixture with Steppe nomads.
- **Key Samples and Anomalies:**
 - **Koban9 (Zayukovo-3):** Carried Y-Haplogroup **G-Z6554 (G2a)**, demonstrating continuity with the local Bronze Age population.¹⁶
 - **Koban8 (Zayukovo-3):** This individual, dated to ~650 BCE, carried Y-Haplogroup

D-CTS10441 (D1a). Haplogroup D is typically found in East Asia (e.g., Tibet, Japan) and is extremely rare in West Eurasia. Its presence in an Iron Age Caucasus burial suggests incredible long-distance individual mobility or the integration of individuals from far-eastern Scythian networks into local elites.¹⁶

- **Sex Correction:** Ancient DNA analysis corrected the biological sex of sample **Klin-Yar III:ID355**, previously identified as male by anthropologists, to female. This underscores the importance of genomic verification in archaeological contexts.¹⁷

6.2 The Scythian World

The recent massive study by *Andreeva et al.* (2025) has clarified the genetic structure of "Great Scythia," covering the area from the Black Sea to the Don.

- **Genetic Structure:** The Scythians were not a homogeneous population. While they shared a cultural package ("Scythian Triad"), their genetics varied by geography.
- **Middle Don Scythians:** This group was predominantly characterized by **R1a-Z93** subclades (specifically **R-Y2631** and **R-Y2**). This lineage connects them to the Bronze Age **Srubnaya** culture but distinct from the earlier Yamnaya lineages. However, *Andreeva et al.* note a lack of direct continuity between the specific Srubnaya lineages of the region and the later Scythians, suggesting the Scythians were newcomers who replaced or assimilated the post-Srubnaya locals rather than evolving directly from them *in situ*.¹⁸
- **Admixture:** Scythian samples consistently show minor but significant **East Asian/Siberian** ancestry, accumulating over time. This confirms the historical narrative of their eastern origins or constant back-migration from the Altai region.
- **Sample DM5:** An outlier from the same region, dated earlier, carried **R1b1a1** and **U5a2** mtDNA. This profile creates a link to Mesolithic European hunter-gatherers, suggesting that pockets of distinct, older ancestries persisted in the forest-steppe zone long after the Neolithic transition elsewhere.¹⁹

6.3 The Alans: Formation of a Confederation

By the first millennium CE, the **Alans** emerged as a powerful confederation in the North Caucasus. Their genetics, analyzed in studies by *Sharko* and *Afanasiev*, reveal a consolidation of lineages.

- **Admixture Profile:** Alanic samples show a fusion of **Haplogroup G2a** (local Caucasus origin) and **R1a/Q** (Steppe origin) lineages.
- **Ossetian Origins:** This specific admixture profile—local Caucasian paternal lines assimilated into an originally Iranian-speaking nomadic confederation—forms the direct genetic ancestry of modern **Ossetians**. The high frequency of G2a in modern Ossetians (>60-70%) despite their Iranian language suggests a process of "elite dominance," where a smaller number of Alanic/Scythian warriors imposed their language and culture on a larger demographic base of local North Caucasians.²⁰

7. Master Table of Ancient Samples (Selected)

The following table synthesizes key samples discussed in the literature (2015-2025) that define the genetic clusters of the region.

Sample ID	Site / Region	Period	Approx . Date	Culture	Y-Hapl ogroup	mtDNA Haplog roup	Refere nce
SATP	Satsurb lia, Georgia	Upper Paleo.	13,000 BP	CHG	J1-FT34 521	K3	1
KK1	Kotias Klde, Georgia	Mesolit hic	9,700 BP	CHG	J2a-Y12 379*	H13c	1
PG200 1	Progres s 2, N. Caucas us	Eneolith ic	4300 BCE	Eneolith ic Steppe	-	I2	4
SA6013	Sharak halsun, Russia	Early Bronze	3360-3 102 BCE	Steppe Maykop	R-YP127 2 (R1a)	I5b	6
OS500 2	Marinsk aya, Russia	Early Bronze	3900 BCE	Maykop Proper	L (likely)	-	4
ARM00 2	Kaps, Armeni a	Early Bronze	3356-31 02 BCE	Kura-Ar axes	G2b (G-Z80 24)	K3	10
VEK00 7	Velikent , Dagestan	Early Bronze	3000 BCE	Kura-Ar axes	J1 (likely)	-	12

I1634	Areni, Armenia	Chalcolithic	4000 BCE	Areni	L1a (L-M76)	H2a1	²³
Koban 9	Zayuko vo-3, Russia	Iron Age	600 BCE	Koban	G2a (G-Z6554)	T1a1	¹⁶
Koban8	Zayuko vo-3, Russia	Iron Age	650 BCE	Koban	D1a (D-CTS 10441)	HV1	¹⁶
DA162	Unknown, Russia	Medieval	450-850 CE	Alan	R1a	-	²⁴
Sc_Mdon	Middle Don, Russia	Iron Age	400 BCE	Scythian	R1a-Z93 (R-Y2631)	Various	¹⁸

Note: "Likely" indicates haplogroup inferred from population-level data in the source where individual ID mapping was implicit.

8. Modern Continuity and Gap Analysis

8.1 Modern Continuity: The "Highland Resilience"

One of the most robust findings of the decade is the resilience of the CHG genetic profile. Despite the massive Bronze Age and Iron Age turnovers in the steppe and lowlands, the high mountain populations retained significant genetic continuity.

- **Genetic Affinity:** As illustrated by comparative Fst analyses (qualitatively summarized here), ancient Koban samples show high affinity to modern **Ossetians**, **Kumyks**, and **Lezgins**. This confirms that the Iron Age population of the North Caucasus did not disappear but evolved into the modern ethnic groups of the region.²⁵
- **The "Zana" Case:** The analysis of Zana from Abkhazia (19th century) served as a control study for modern continuity. Her genome was purely East African, unrelated to ancient or modern Abkhazians (who carry G2a/J2 lineages). This demonstrated that while the region has deep continuity, it also integrated individuals from long-distance historical trade/slave networks.²⁶

8.2 Gap Analysis: The Missing Pieces

Despite the progress, significant gaps remain:

1. **The "Urartian" Void:** We lack a high-resolution transect of the Urartian ruling elite. Understanding their biological kinship is crucial to resolving the relationship between the Hurro-Urartian and Nakh-Dagestanian language families.
2. **The Maikop-Steppe Interface:** The precise mechanism of coexistence between the genetically distinct "Steppe Maykop" and "Maykop Proper" populations remains unclear. Did they intermarry? Did they speak different languages? The current data shows separation, but the "border zones" are undersampled.
3. **Southern Slope Neolithic:** Data from the Neolithic of Azerbaijan is sparse compared to Armenia and Georgia, obscuring the eastern route of the Neolithic expansion.

9. Conclusion

The decade of research from 2015 to 2025 has transformed the Caucasus from a black box of prehistory into one of the most genetically characterized regions on Earth. The data confirms the region's dual nature: it was a **barrier** that preserved the deep CHG ancestry for millennia, allowing for the isolation of the Kartvelian and Nakh-Dagestanian language families. Simultaneously, it was a **bridge**—first for the northward expansion of Neolithic farmers who created the Maykop culture, and later for the southward pulses of Steppe pastoralists who likely brought Indo-European languages to the Armenian Highlands.

The identification of the **Steppe Maykop** as a distinct genetic entity and the confirmation of **Koban-Alan-Ossetian** continuity are among the most significant specific findings. As we move forward, the integration of this genomic data with proteomic and isotopic analyses promises to reveal not just *who* these people were, but *how* they lived, establishing a fully bio-archaeological history of the Caucasus.

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