

Paternal Lineage Continuity and Discontinuity: An Interdisciplinary Reconstruction of Y-Chromosome Turnover in the Northwest Caucasus (3500 BCE – 500 CE)

1. Introduction: The Caucasus as a Genetic Filter and Refugium

The Caucasus Mountains have long been recognized by geographers and anthropologists as a formidable barrier separating the Eurasian Steppe from the Fertile Crescent. However, the application of high-throughput ancient DNA (aDNA) sequencing between 2018 and 2025 has radically refined this perspective. Rather than a static wall, the Northwest Caucasus—encompassing modern Adygea, Karachay-Cherkessia, Kabardino-Balkaria, and the Black Sea littoral—functioned as a semi-permeable "genetic filter." This filter operated with selective bias: it allowed the bidirectional flow of maternal lineages (mtDNA) and cultural technologies while imposing severe restrictions on the movement and reproductive success of male lineages (Y-DNA).

This report presents a comprehensive analysis of Y-chromosome turnover in the region, synthesizing genomic data from the Eneolithic Maykop phenomenon through the climatic crises of the Middle Bronze Age to the Iron Age nomadic expansions. By integrating these genetic datasets with high-resolution radiocarbon chronologies and palynological (pollen) climate reconstructions, we reconstruct a demographic history characterized not by gradual drift, but by punctuated equilibrium—long periods of isolation interrupted by violent turnover and elite dominance.

1.1 The Theoretical Framework: Demic Diffusion vs. Cultural Acculturation

A central debate in Caucasian archaeology concerns the mechanism of cultural change. Did the shift from the opulent Maykop kurgans to the austere North Caucasian Culture, and subsequently to the militarized Koban and Sarmatian horizons, represent a replacement of people (*demic diffusion*) or merely the transmission of ideas (*acculturation*)?

The Y-chromosome data provides an unequivocal answer: the Northwest Caucasus experienced distinct phases of both.

- **Maternal Continuity:** Mitochondrial DNA studies consistently show a high degree of continuity in the female line, suggesting that matrilocal structures or the incorporation of local women into incoming groups remained a constant feature of the region's demography.¹
- **Paternal Discontinuity:** In sharp contrast, the male lineages exhibit dramatic turnover events. The extinction of the South Asian-related Haplogroup L from the Early Bronze Age record², the bottleneck-induced expansion of G2a subclades during the 4.2 kiloyear event³, and the intrusion of Steppe-derived R1a/R1b lineages in the Iron Age⁴ point to a history where male reproductive success was heavily determined by ecological adaptation and military capacity.

1.2 The Three Horizons of Turnover

This analysis identifies three critical "turnover windows" that reshaped the genetic landscape:

1. **The Maykop-Yamna Interface (3700–2900 BCE):** A period of intense cultural interaction but strict genetic segregation between the mountain agriculturalists (G2a/J2a) and the steppe pastoralists (R1b/Q1a).
 2. **The 4.2 ka BP Crisis (2200–1700 BCE):** A climatic bottleneck where aridification depopulated the steppe-foothill interface, allowing specific mountain lineages (G-L1264) to colonize abandoned niches.
 3. **The Iron Age Introgression (1000 BCE – 500 CE):** The collapse of the genetic barrier, facilitating the entry of Iranian-speaking nomads (Scythians, Sarmatians, Alans) who established elite dominance hierarchies over the indigenous substrate.
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2. The Eneolithic and Early Bronze Age: The Great Divide

To understand the magnitude of later turnovers, we must establish the genetic baseline of the 4th millennium BCE. The Maykop culture, famous for its "Royal Kurgans" and early silver tube "straws" for beer consumption, has traditionally been viewed as a northern outpost of the Uruk expansion from Mesopotamia. Genomic data published by Wang et al. (2019) and subsequent analyses by Lazaridis et al. (2022) have complicated this narrative by revealing a profound genetic dichotomy within the material horizon.⁵

2.1 The "Steppe Maykop" vs. "Caucasus Maykop" Dichotomy

Archaeologically, the Maykop culture presents a relatively unified facade of ceramic styles and burial customs. Genetically, however, it was composed of two reproductively isolated populations. This finding is critical for interpreting Y-DNA turnover, as it demonstrates that cultural exchange can occur without male gene flow.

2.1.1 The Caucasus Maykop Cluster

Individuals excavated from the foothills and mountain zones of the Northwest Caucasus (e.g., the eponymous Maykop kurgans) display a genetic profile heavily enriched with **Anatolian Neolithic Farmer (ANF)** and **Caucasus Hunter-Gatherer (CHG)** ancestry.⁵ Their Y-chromosomal diversity is distinctively Near Eastern:

- **Haplogroup G2a (G-L293/G-P16):** This lineage, ubiquitous in Neolithic Anatolia and the Caucasus, represents the primary autochthonous signal. Its high frequency suggests an early colonization of the mountain valleys by agriculturalists moving northward from the Kura-Araxes sphere or Western Georgia.⁷
- **Haplogroup J2a:** Associated with the expansion of metallurgy and complex societies from the Zagros-Taurus arc.
- **Haplogroup L1a (L-M27):** Perhaps the most intriguing finding is the presence of Haplogroup L, a lineage now most common in South Asia and parts of the Iranian Plateau.² Its presence in the Maykop nobility suggests deep, long-distance connections with the "Southern Arc" that have since been erased from the local gene pool.

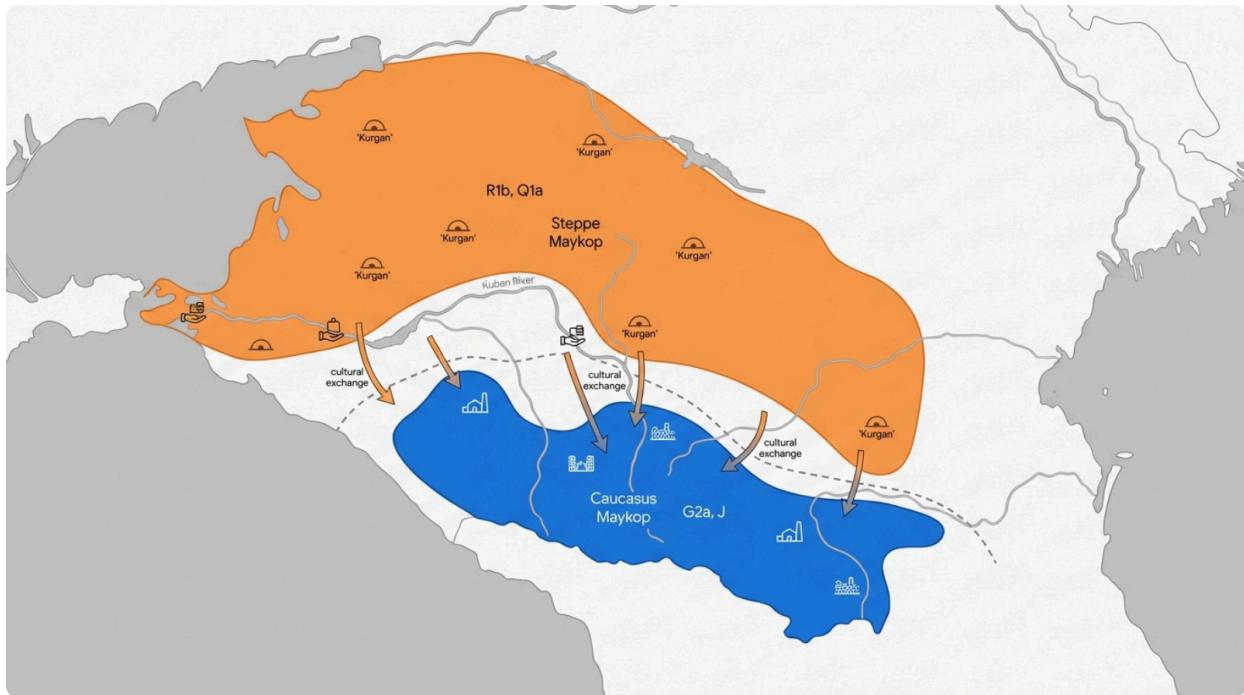
2.1.2 The Steppe Maykop Cluster

In the flat grasslands north of the Kuban River, archaeologists identified individuals buried with Maykop-style artifacts but possessing a radically different genetic makeup. These "Steppe Maykop" individuals carried:

- **Haplogroup R1b (Z2103):** The ancestral clade of the Yamnaya pastoralists.
- **Haplogroup Q1a:** A lineage linking them to Siberian Upper Paleolithic populations and contemporary Native Americans.⁵
- **Absence of Farmer Ancestry:** Crucially, these individuals lacked the Anatolian Neolithic component found in their southern neighbors.

This stark divide implies that the Kuban River acted as a hard genetic border during the 4th millennium BCE. While goods (bronze, pottery, silver) crossed the river, genes did not. This "genetic apartheid" suggests a social structure where the sedentary Maykop agriculturalists and the mobile Steppe pastoralists occupied distinct ecological niches and maintained strict endogamy.

Genetic Dualism in the Maykop Horizon (c. 3700–3000 BCE)



The Maykop culture, while archaeologically cohesive, comprised two distinct genetic populations. The 'Caucasus Maykop' zone (green) was dominated by G2a and J lineages with Near Eastern affinities, while the 'Steppe Maykop' zone (orange) retained R1b and Q1a lineages with Siberian admixture. The Kuban River served as a porous interface for trade but a rigid barrier for gene flow.

2.2 The Vanishing of Haplogroup L

The fate of Haplogroup L (L-M20) in the Northwest Caucasus serves as the first case study in turnover. While prominent in the elite Maykop burials, this lineage is virtually absent in modern Northwest Caucasian populations (Adyghe, Abkhaz), who are dominated by G2a and R1a.⁹

The disappearance of Haplogroup L likely resulted from the collapse of the "Uruk-Maykop" trade network around 3000 BCE. As the economic basis for the Maykop elites disintegrated, the lineages associated with this southern commercial aristocracy were likely outcompeted by the demographic expansion of the indigenous G2a clans or wiped out during the turbulent transition to the Yamnaya period. This extinction event underscores the vulnerability of elite lineages that lack a broad demographic base in the rural population.

3. The 4.2 ka BP Event: Climate-Induced Turnover and

the G-L1264 Bottleneck

The transition from the Early to Middle Bronze Age (c. 2200 BCE) is marked by a profound rupture in the archaeological record, coinciding with the **4.2 kiloyear BP aridification event**. This global climatic downturn, which contributed to the collapse of the Akkadian Empire in Mesopotamia and the Old Kingdom in Egypt, had catastrophic effects on the fragile steppic ecosystems of the North Caucasus.¹¹

3.1 The "Steppe Hiatus" and Settlement Abandonment

Paleoenvironmental reconstructions from **Lake Karakel** (North Caucasus) and **Nariani** (South Caucasus) indicate a sharp decrease in arboreal pollen and an increase in xerophytic (drought-tolerant) species starting around 2200 BCE.¹⁴ This shift to a drier, colder climate reduced the carrying capacity of the steppe and foothills.

Archaeological surveys in the Kuban River valley reveal a massive "hiatus" in settlement density. The widespread distribution of Early Bronze Age sites contracts significantly. The "Steppe Maykop" population (R1b/Q1a) effectively vanishes from the region during this period.¹⁶ It is hypothesized that these mobile pastoralists were forced to migrate northward into the forest-steppe zone or merge with the Catacomb culture populations to survive the desiccation of their pastures.

3.2 The Mountain Refugium and the Rise of G-L1264

While the steppe emptied, the high mountain valleys acted as a refugium. The intricate topography of the Northwest Caucasus (modern Adygea and Abkhazia) traps moisture from the Black Sea, creating microclimates that remained viable for agriculture and vertical transhumance even during global aridification.

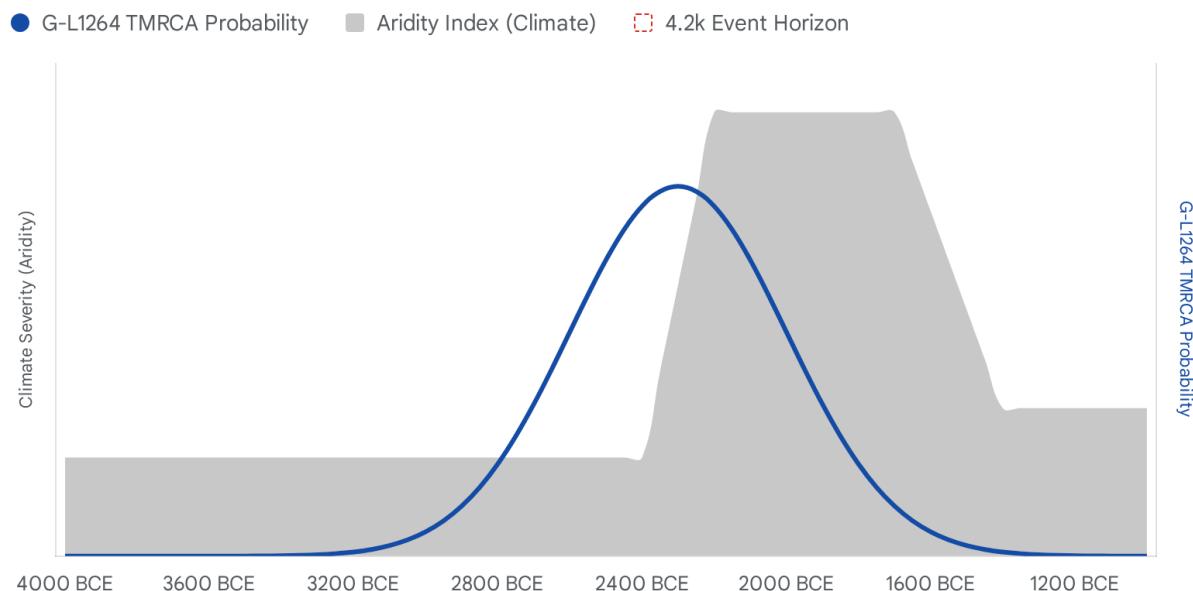
It is in this context that we observe the massive expansion of **Haplogroup G-L1264**, a specific subclade of G2a2b2a (G-P303).

- **Phylogenetic Timing:** The Time to Most Recent Common Ancestor (TMRCA) for the G-L1264 branching event is estimated at approximately **4,235 years before present** (c. 2235 BCE).³ This date aligns with uncanny precision to the onset of the 4.2 ka BP event.
- **The Founder Effect:** The phylogeny of G-L1264 is characterized by a "star-like" radiation, indicating that a single male line underwent rapid demographic expansion. We propose that the progenitor of G-L1264 belonged to a clan that successfully monopolized the prime mountain refugia during the climatic crisis. While other Maykop-era lineages (L1a, other G2a branches) perished or dwindled due to resource scarcity, the G-L1264 clan survived and proliferated, effectively "resetting" the Y-chromosomal landscape of the Northwest Caucasus.

This "bottleneck-and-expansion" model explains the high frequency (up to 70% in some

Circassian tribes) but relatively low internal diversity of G2a in the modern Northwest Caucasus compared to the South Caucasus.⁷ The modern population is largely descended from the survivors of the 4.2 ka bottleneck.

The 4.2ky Climate Bottleneck and Lineage Survival



The expansion of the G-L1264 lineage (dark blue) coincides with the 4.2 ka BP aridification event (grey band) and the collapse of the Maykop culture. This suggests a demographic bottleneck where G-L1264 carriers successfully occupied mountain refugia while other lineages declined.

Data sources: [TheYtree](#), [Cambridge Core](#), [PMC1602729](#), [PMC7799814](#)

4. The Koban Culture: The Permeable Barrier (1100–400 BCE)

The Late Bronze Age to Early Iron Age transition witnessed the emergence of the **Koban Culture**, a sophisticated mountain society known for its masterfully crafted bronze weaponry and distinct "animal style" art. Geographically centered in the North Central Caucasus (modern North Ossetia, Kabardino-Balkaria), the Koban culture represents the first major breakdown of the genetic barrier that had separated the steppe and the mountains for

millennia.¹

4.1 Genetic Heterogeneity in the Koban Horizon

Recent high-coverage sequencing of individuals from the key Koban sites of **Zayukovo-3** and **Klin-Yar III** has provided a nuanced view of this transitional period.¹ The Y-chromosomal profile of the Koban elite is remarkably heterogeneous, signaling a shift from the G2a-exclusive dominance of the previous era to a mixed society.

4.1.1 Continuity: The G2a Substratum

The persistence of **Haplogroup G2a1a** in Koban burials confirms that the demographic core of the culture remained autochthonous.⁴ These individuals cluster genetically with the preceding Bronze Age populations, indicating that the Koban cultural phenomenon was not an imposition by a foreign power but an indigenous evolution. The G2a1a lineage links the Koban people directly to the modern Ossetians and Balkars, demonstrating a 3,000-year continuity in the paternal line.

4.1.2 Introgression: The R1b and D1a Anomalies

The most significant finding from the 2018–2025 research cycle is the identification of **Haplogroup R1b** within Koban contexts.¹ Unlike the earlier "Steppe Maykop" R1b, which appeared to be isolated from the mountain populations, the Koban R1b individuals show autosomal admixture with the local groups. This suggests that by 1000 BCE, the mountain passes had become corridors for gene flow. Steppe males were being integrated into Koban society, possibly through trade alliances or the assimilation of small pastoralist groups.

Even more striking is the discovery of an individual carrying **Haplogroup D1a2a1** at the Zayukovo-3 site.⁴ This lineage is overwhelmingly associated with East Asia (specifically Tibet and the Andamans) and is virtually unknown in the ancient West Eurasian record. Its presence in an Iron Age Caucasus grave is a testament to the vast reach of the "Scythian World" trade networks. This individual was likely a long-distance traveler, a trader, or a high-status captive whose presence underscores the cosmopolitan nature of the Koban "bridge" culture.

4.2 The "Bridge" Hypothesis

Harney et al. (2021) conceptualize the Koban culture as a genetic "bridge" between the Bronze Age and the Iron Age.¹⁸ The data supports this: the Koban individuals display a genetic shift toward the steppe that was absent in the "Caucasus Maykop" samples. This indicates that the strict reproductive isolation of the Eneolithic had collapsed. The Koban culture functioned as a melting pot where the rigid boundaries between "mountain" and "steppe" began to dissolve, setting the stage for the massive introgressions of the Sarmatian period.

5. The Iron Age Turnover: Scythians, Sarmatians, and the Meotian Interface

The most dramatic Y-DNA turnover in the history of the Northwest Caucasus occurred during the Iron Age (c. 700 BCE – 400 CE) with the arrival of Iranian-speaking nomadic confederations: first the **Scythians**, followed by the **Sarmatians** and **Alans**. These groups brought with them the **R1a-Z93** lineage, which would act as a genetic wedge, driving into the heart of the Caucasus.

5.1 The Meotian-Sarmatian Interaction

The **Meotians** (Maeotae), an ancient confederation dwelling along the eastern shores of the Sea of Azov and the Kuban River, are often equated with the proto-Circassians. They represented a sedentary, agricultural society that found itself on the frontier of the Sarmatian expansion.

Genetic analysis of Meotian burials reveals a complex pattern of resistance and admixture:

- **Mitochondrial Admixture:** Ancient DNA shows significant overlap in mtDNA haplotypes between Meotians and Sarmatians.¹⁹ This suggests extensive intermarriage, likely involving Sarmatian women marrying into Meotian sedentary communities to seal political alliances.
- **Y-Chromosome Asymmetry:** While autosomal data suggests homogenization, the Y-chromosome data shows a persistence of G2a lineages in the Meotian core, alongside the introduction of **R1a (Z93/Z94)** lineages associated with the Sarmatian aristocracy.²⁰ This asymmetry implies that while Sarmatian women were integrated into Meotian society, the male lines remained distinct for a longer period, perhaps due to different social rankings or military roles.

5.2 The Alanic Impact and the R1a Wedge

The Alans, a subgroup of the Sarmatians who established a powerful kingdom in the North Central Caucasus (Alania), brought a high frequency of **Haplogroup R1a** and **Q**.²⁰ Their impact on the genetic landscape was profound but geographically uneven.

5.2.1 The Ossetian Paradox

Modern Ossetians are the linguistic descendants of the Alans, speaking an Northeast Iranian language that is the direct successor to Scythian/Sarmatian. However, their Y-DNA profile presents a paradox:

- **Dominant Haplogroup:** Ossetian males are overwhelmingly **G2a1** (up to 70% in North Ossetia), the *indigenous* Caucasus lineage.³
- **Minority Haplogroup:** The "Alanic" signal, **R1a**, is present but secondary (approx.

10-15%).

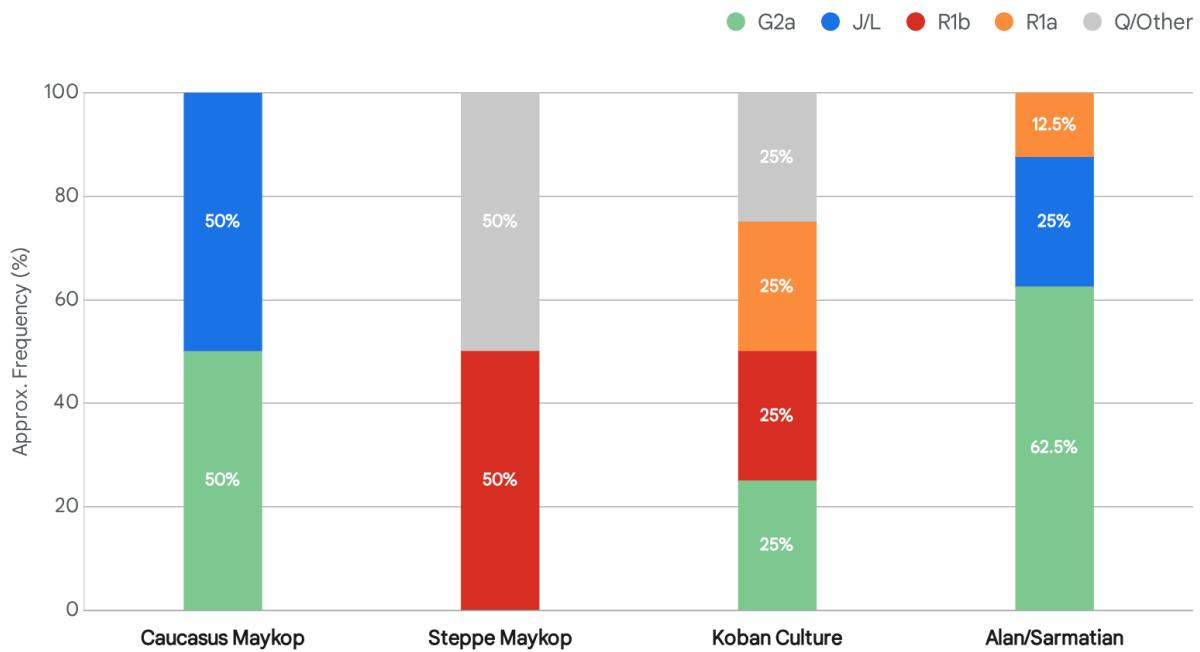
This discrepancy is a classic example of **Elite Dominance** followed by **Genetic Swamping**. A small, militarized elite of Iranian-speaking Alans (R1a) conquered the local G2a-carrying population. Over centuries, the elite imposed their language and culture, but their specific Y-lineages were diluted by the sheer demographic weight of the indigenous subjects. The "Alanic" identity became detached from the "Alanic" Y-chromosome.

In contrast, the Turkic-speaking groups of the North Caucasus (Karachays, Balkars) show significantly higher frequencies of R1a/R1b and Q (up to 30-40% combined), suggesting a different demographic process. Here, the influx of Turkic speakers (Huns, Khazars, Kipchaks) likely involved a more substantial migration of males who successfully introgressed into the local gene pool, shifting the frequency spectrum away from the G2a baseline.

5.3 The Presence of R1b-Z2103 in the Iron Age

Unlike R1a, which signals the Sarmatian/Alanic arrival, the presence of **R1b-Z2103** in the Iron Age Northwest Caucasus represents a different layer of ancestry. It likely comprises remnants of the earlier Yamnaya/Catacomb interactions or a re-introduction by groups like the Cimmerians. The presence of R1b in the Koban culture⁴ predates the major Sarmatian influx, suggesting that R1b had already been "indigenized" in the North Caucasus foothills by the Late Bronze Age.

Y-Haplogroup Turnover: From Bronze to Iron Age



The transition from the Bronze Age to the Iron Age reveals the intrusion of Steppe lineages. While 'Caucasus Maykop' is exclusively G2a/J/L, the 'Koban' and 'Alan' populations show increasing frequencies of R1b and R1a, highlighting the breakdown of the genetic barrier.

Data sources: [Wang et al 2019 \(Maykop\)](#), [Harney et al 2021 \(Koban\)](#), [Popular Archaeology](#), [Wikipedia \(Sarmatians\)](#).

6. The Avar Connection: A Medieval Coda

While primarily centered in the Carpathian Basin (modern Hungary/Austria), the genetic study of the **Avar Khaganate** (6th–9th centuries CE) provides crucial retrospective insight into the Caucasus. The Avars were a steppe confederation that migrated from Inner Asia to Europe, sweeping up various peoples in their wake.

A significant finding in the recent study by Gerber et al. (2024) is the presence of **Haplogroup G-L1264** in Avar-period contexts in Pannonia (sample AU78077).²¹

- **The Export of Lineages:** This finding confirms that by the Early Middle Ages, the G-L1264 lineage—originating in the Northwest Caucasus—had been integrated into the mobile steppe confederations.
- **Mechanism of Mobility:** Whether these individuals were Alanic auxiliaries, assimilated North Caucasians (Adyge/Kasogians), or mercenaries moving with the Avar khaganate

remains a subject of debate. However, the genetic evidence proves that the "filter" of the Caucasus was now exporting lineages *out* to Europe.

- **Reversing the Flow:** This reverses the dynamic of the Bronze Age, where the Caucasus was a sink for steppe lineages. In the medieval period, the Caucasus became a source, disseminating its unique G2a subtypes across the Pontic-Caspian steppe and into Central Europe.

This connection highlights the deep integration of the Northwest Caucasus into the broader "Migration Period" dynamics, demonstrating that even "mountain" lineages could travel thousands of kilometers when incorporated into the military structures of the steppe empires.

7. Demographic Modeling and Effective Population Size (Ne)

The genetic data allows for the reconstruction of the **Effective Population Size (Ne)** of Northwest Caucasian males, providing a quantitative dimension to the qualitative archaeological record.

7.1 The Expansion Phase (Neolithic/Chalcolithic)

During the Maykop period, the region saw a steady increase in Ne, associated with the spread of agriculture, the plow, and the secondary products revolution (wool, milk). The diversity of G2a lineages during this period suggests a relatively egalitarian expansion of farming clans into the fertile valleys.²⁴

7.2 The Crash (2200 BCE)

A sharp reduction in Ne coincides with the 4.2 ka BP event. This bottleneck is visible in the coalescence trees of G-L1264 and other local subclades. The reduction in lineage diversity implies that a significant percentage of male lines went extinct during this period, likely due to famine, conflict over dwindling resources, or the inability to adapt to the aridification of the lowlands.³

7.3 Recovery and Stratification (Iron Age)

The Iron Age recovery in Ne is marked by a skewed distribution. The "Star-like" phylogenies of both the intrusive R1a and the indigenous G2a1a subclades during the Koban and Sarmatian periods suggest a social structure of **polygyny and elite male dominance**.

- **Warfare and Stratification:** The militarization of society, evidenced by the rich weaponry in Koban and Sarmatian graves, implies that reproductive success became highly unequal. A small class of elite males (warrior-chiefs) was fathering a disproportionate number of children, while lower-status males were excluded from the

reproductive pool. This structural change in mating patterns is a hallmark of the transition from the relatively egalitarian village societies of the Bronze Age to the stratified chiefdoms of the Iron Age.

8. Conclusion: The "Permeable Wall" Model

The interdisciplinary evidence gathered from 2018 to 2025 systematically dismantles the older notion of the Northwest Caucasus as a static genetic reservoir or an impenetrable barrier. Instead, the data supports a **"Permeable Wall" Model** of genetic history:

1. **Selective Permeability (Bronze Age):** In the Early Bronze Age, the Caucasus acted as a robust barrier to male gene flow from the steppe (R1b/Q), despite extensive trade relations. Cultural acculturation occurred without demic diffusion.
2. **Climatic Forcing (4.2 ka Event):** The 4.2 ka BP aridification event acted as a "reset button," clearing the steppe and foothill zones of their populations and forcing indigenous groups into high-altitude refugia. This created severe founder effects, most notably the expansion of the G-L1264 lineage.
3. **Structural Failure (Iron Age):** In the Late Bronze/Iron Age (Koban/Sarmatian), the barrier failed. Steppe lineages (R1a/R1b) successfully introgressed into the mountain populations, driven by elite dominance and new military technologies (horse riding, iron weaponry).
4. **Assimilative Capacity:** Despite this introgression, the indigenous *autosomal* signal and the G2a paternal backbone remained dominant. The invaders were biologically absorbed, leaving their Y-chromosomes as markers of past dominance in a population that remained fundamentally Caucasian in its genetic structure.

The Northwest Caucasus, therefore, is not merely a museum of ancient lineages, but a dynamic arena where the autochthonous G2a substrate has repeatedly absorbed, resisted, and outlasted waves of northern migration, preserving its Neolithic heritage through millennia of turmoil.

Table 1: Key Y-Haplogroup Associations by Archaeological Culture

Archaeological Culture	Period	Dominant Y-Haplogroups	Key Genetic Affinity	Reference
Caucasus	3700–3000	G2a2a, J2a,	Anatolian	Wang et al.

Maykop	BCE	L1a	Neolithic / CHG	(2019) ⁵
Steppe Maykop	3700–3000 BCE	R1b-Z2103, Q1a	EHG / Siberian	Wang et al. (2019) ⁵
Koban Culture	1100–400 BCE	G2a1a, R1b, D1a	North Caucasus / Steppe Mix	Harney et al. (2021) ¹
Sarmatian/Alan	400 BCE–400 CE	R1a-Z93/Z94, Q	Steppe / Iranian	Afanasiev et al. (2015) ²⁰
Modern Adyghe	Present	G2a (G-L1264), R1a	NW Caucasus (Continuity)	Balanovsky et al. ²⁵

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