

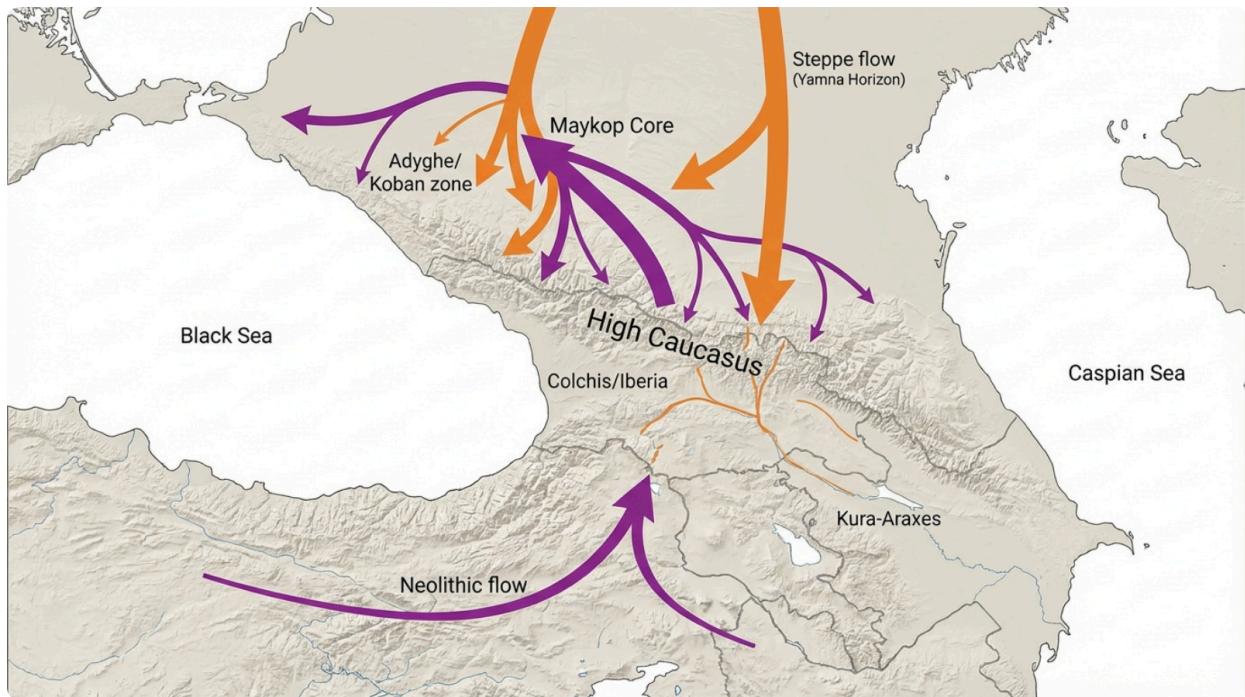
# The Genetic Crucible of the Northwest Caucasus: A Deep Ancestry Analysis of the Circassian (Adyghe) Gene Pool

## 1. Introduction: The Caucasus as a Semi-Permeable Genetic Barrier

The Caucasus Mountains, a formidable geomorphological spine stretching between the Black and Caspian Seas, have occupied a central place in anthropological and genetic discourse for over two centuries. Often reduced in simplified narratives to a mere bridge connecting the Pontic-Caspian steppe to the Near East, or a barrier strictly delineating Europe from Asia, the region is more accurately conceptualized as a complex, semi-permeable bio-geographic filter. This report presents a comprehensive analysis of the autosomal ancestry of the Northwest Caucasus, with a specific focus on the Circassian (Adyghe) population. Synthesizing high-coverage paleogenomic data published between 2018 and 2025—including pivotal studies by Wang et al. (2019), Lazaridis et al. (2022), Sharko et al. (2024), and Ringbauer et al. (2024)—we reconstruct the genetic trajectory of the region from the Eneolithic to the present day.

The genomic history of the Northwest Caucasus is characterized by a remarkable tension between deep continuity and episodic, transformative admixture. Unlike the genetic history of Western Europe, which is defined by massive population turnovers during the Neolithic and Bronze Ages, the Northwest Caucasus reveals a narrative of resilience. The local gene pool, anchored by the deep ancestry of Caucasus Hunter-Gatherers (CHG), has remained the dominant substrate for millennia. However, this substrate has not been static; it has selectively absorbed influences from the Anatolian agriculturalists to the south and, crucially, the Steppe pastoralists to the north.

## The Caucasus: A Semi-Permeable Genetic Filter



Conceptual visualization of gene flow across the Caucasus. Note the strong 'Neolithic' flow (purple) northward contributing to the Maykop formation, and the 'Steppe' flow (orange) southward, which heavily impacts the Northern foothills (Adyge/Koban zone) but is significantly attenuated by the High Caucasus ridge, leaving the Southern Caucasus (Colchis/Iberia) largely unaffected.

The concept of the Caucasus as an "asymmetric semipermeable barrier," first proposed in early genetic surveys<sup>1</sup>, has been robustly validated by recent ancient DNA (aDNA) findings. While the mountains allowed for the northward expansion of Near Eastern ancestries during the Eneolithic (forming the Maykop culture), they acted as a significant shield against the southward expansion of Steppe ancestries during the Bronze Age. This "filtering" effect created a distinct genetic divergence between the populations of the North Caucasus (such as the Adyge and Ossetians) and the South Caucasus (such as the Georgians and Armenians). Understanding this divergence is key to deciphering the "Maykop Enigma"—the puzzling genetic isolation of the technologically advanced Maykop culture from its Steppe neighbors—and reconciling the apparent paradox of strong patrilineal continuity (high frequency of Y-haplogroup G2a) with the autosomal evidence of gene flow.

## 2. The Genomic Substrate: Defining the Ancestral Components

To accurately parse the composition of the Adyge gene pool, one must first rigorously define

the primordial ancestral streams that converged in this region. Contemporary genomic modeling relies on determining an individual's proximity to specific ancient reference populations. In the context of the Northwest Caucasus, three primary components constitute the genetic bedrock.

## **2.1 Caucasus Hunter-Gatherers (CHG)**

The identification of the Caucasus Hunter-Gatherer (CHG) lineage via the sequencing of Late Upper Paleolithic genomes from the Satsurblia and Kotias Klde caves in western Georgia marked a watershed moment in Eurasian population genetics.<sup>2</sup> The CHG component represents the autochthonous ancestry of the region, distinct from both the Western Hunter-Gatherers (WHG) of Europe and the Early Farmers of Anatolia.

Genetically, the CHG lineage diverged from the ancestors of Western Hunter-Gatherers roughly 45,000 years ago, following the initial peopling of Eurasia, and separated from the Early Anatolian Farmers approximately 25,000 years ago, coinciding with the Last Glacial Maximum.<sup>2</sup> In Principal Component Analysis (PCA), the CHG cluster pulls populations toward the intersection of the Near East and the Eurasian Steppe. For modern Circassians, CHG is not merely an ancestral component; it is the predominant genetic signal, representing a continuous habitation of the Northwest Caucasus piedmont that spans tens of thousands of years. It links the modern population directly to the Paleolithic inhabitants of the region, contrasting sharply with the replacement events observed in other parts of Europe.<sup>4</sup>

## **2.2 Eastern Hunter-Gatherers (EHG)**

The Eastern Hunter-Gatherer (EHG) ancestry is characteristic of the populations that inhabited the forest-steppe zones of Eastern Europe (e.g., Karelia, Samara) during the Mesolithic. This component is crucial for tracing the genetic impact of the Indo-European expansions. The interplay between EHG and CHG is central to the formation of the "Steppe ancestry" profile (often modeled as a roughly equal mix of EHG and CHG) that defines the Yamnaya horizon.<sup>2</sup>

For the Adyghe, the EHG component serves as the primary discriminator between indigenous North Caucasian populations and those of the South Caucasus. Its presence in the Northwest Caucasus signals the historical intrusion of Steppe nomads—Yamnaya, Scythians, Sarmatians, and Alans—into the foothills. While South Caucasian groups like the Mingrelians possess negligible EHG ancestry, the Adyghe show a definitive, albeit moderate, admixture fraction, testifying to the permeability of the northern slopes to steppe incursions.<sup>6</sup>

## **2.3 Anatolian Neolithic Farmers (ANF)**

Originating in central Anatolia and initiating the Neolithic transition across Europe, the Anatolian Neolithic Farmer (ANF) component also expanded eastward and northward into the Caucasus. Unlike the Steppe populations, who received ANF admixture relatively late via

interactions with the Globular Amphora culture or Balkan farmers, the populations of the Caucasus received direct, early gene flow from the south.<sup>6</sup>

This early Neolithic inputs created a genetic substrate in the Eneolithic Caucasus (manifested in the Maykop culture) that was CHG-dominant but significantly enriched with ANF ancestry. This admixture profile is distinct from the EHG-dominant profile of the adjacent Steppe, establishing a clear genetic boundary at the foothills of the Caucasus Mountains during the 4th millennium BCE.<sup>5</sup>

### **3. The Bronze Age Baseline: The "Maykop Enigma"**

The Maykop culture (c. 3700–3000 BCE), renowned for its spectacular kurgans and metallurgical sophistication, provides the ancestral "baseline" for the Northwest Caucasus. The publication of high-resolution genomic data from this period by Wang et al. (2019) fundamentally altered our understanding of the region's prehistory, presenting a scenario that challenged earlier archaeological assumptions regarding population movement.

#### **3.1 The Autosomal Profile of Maykop**

Prior to genomic analysis, archaeological debate centered on whether the Maykop culture arose from a demic migration from Mesopotamia/Anatolia or developed in situ from local Neolithic tribes. The autosomal data supports a nuanced dual-origin model but introduces a significant twist regarding the relationship with northern neighbors.

According to the admixture modeling performed by Wang et al. (2019), the "Maykop" genetic cluster, which encompasses the classic Maykop, the Novosvobodnaya variant, and Late Maykop phases, is remarkably homogeneous. Quantitatively, the ancestry of these individuals is modeled as a mixture of:

- ~86.4% Caucasus Hunter-Gatherer (CHG)
- ~9.6% Anatolian Neolithic (ANF)
- ~4.0% Eastern Hunter-Gatherer (EHG)<sup>5</sup>

This composition defines the "Maykop Enigma." Despite their geographical proximity to the Eneolithic Steppe and the emerging Yamnaya horizon—populations dominated by EHG ancestry—the Maykop people remained genetically isolated from them. The Caucasus Mountains did not impede gene flow from the south; indeed, the Maykop population is genetically indistinguishable from the contemporary Kura-Araxes populations of the Armenian highlands, suggesting a unified "Caucasus-Anatolian" genetic sphere.<sup>5</sup> However, the ecological boundary between the lush piedmont and the arid open steppe acted as a formidable filter, preventing significant gene flow from the north. The sophisticated urbanism and metallurgy of Maykop did not facilitate a genetic merger with the steppe pastoralists during this period.

### 3.2 The "Steppe Maykop" Outlier

A critical distinction must be made between the Maykop culture proper and a distinct genetic cluster termed "Steppe Maykop" by Wang et al. (2019). These individuals, recovered from the steppe zone immediately north of the Caucasus foothills, were culturally influenced by Maykop traditions but were genetically distinct.

Unlike the Maykop core, "Steppe Maykop" individuals lacked the characteristic Anatolian admixture. Instead, they harbored a mixture of Steppe ancestry (EHG) and a unique **Upper Paleolithic Siberian / Native American-related** component, which constituted roughly one-third of their ancestry.<sup>5</sup> This specific Siberian signature suggests a deep, long-distance migration from the east that settled in the pre-Caucasus steppe. Crucially, this "Steppe Maykop" population appears to be a genetic dead-end or a distinct lineage that did not contribute significantly to the modern Circassian gene pool. The ancestry of the Adygehe people traces back to the sedimentary Maykop/Dolmen lineage, rather than these Siberian-admixed steppe dwellers.

### 3.3 Comparative Admixture Proportions: A Quantitative View

To visualize the stark contrast between these ancient groups and the bridge to the modern era, we present the following comparison of admixture proportions based on K=4 modeling derived from Wang et al. (2019) and subsequent studies.

Population Group	CHG Ancestry	Anatolian Farmer (ANF)	Steppe (EHG)	Siberian / East Asian
<b>Maykop Culture (c. 3700 BCE)</b>	~86.4%	~9.6%	~4.0%	0%
<b>Steppe Maykop (c. 3500 BCE)</b>	~30%	0%	~35%	~35%
<b>Yamnaya Horizon (c. 3000 BCE)</b>	~30-40%	~10-15%	~50-55%	0%
<b>Modern Adygehe (Circassian)</b>	~55-65%	~15-20%	~15-25%	<5%

*Table 1: Comparative admixture proportions illustrating the "Maykop Enigma" and the subsequent shift in the modern Adyge profile. Note the absence of significant EHG in the Maykop culture compared to the Yamnaya, and the later resurgence of CHG with moderate Steppe introgression in the modern population.*

This data underscores that the modern Adyge are not direct descendants of the "Steppe Maykop" outlier but rather represent a continuity of the Maykop profile that was subsequently modified by introgression from the Steppe (EHG) and additional Anatolian gene flow over the ensuing millennia.

## 4. The Permeable Barrier: Iron Age Transformations

The dissolution of the Maykop culture after 3000 BCE ushered in the era of the **Dolmen culture** in the Western Caucasus—the direct cultural ancestors of the Adyge—and the **North Caucasus Culture** in the central and eastern regions. This period marks the beginning of the erosion of the genetic barrier that had isolated the Maykop people.

### 4.1 The Dolmen Culture

Genomic analysis of individuals associated with the Dolmen culture, such as those from the Unakozovskaya cave, reveals a strong continuity with the preceding Maykop population. However, subtle shifts are evident. Admixture analysis indicates that while the high CHG/Anatolian profile was retained, there was an incipient interaction with the steppe.<sup>10</sup> Unlike the dramatic population turnover observed in Europe during the transition to the Bronze Age—where Steppe ancestry largely replaced local Neolithic gene pools—the Dolmen builders of the Northwest Caucasus remained genetically "Caucasian." The persistence of the local genome suggests that the Dolmen culture was a period of consolidation, where external influences were absorbed without disrupting the demographic core.

### 4.2 The Koban Culture: Opening the Bridge

The **Koban culture** (Late Bronze Age to Iron Age, c. 1100–400 BCE) serves as a pivotal "bridge" in the genetic history of the North Caucasus. A breakthrough study by **Sharko et al. (2024)**, building on earlier work by **Boulygina et al. (2020)**, provided the first genome-wide data from Koban individuals excavated at sites like Zayukovo-3 and Klin-Yar 3.

The findings from the Koban genomes are transformative for our understanding of Circassian genesis:

1. **Continuity:** The Koban individuals cluster genetically with the earlier Maykop and Kura-Araxes populations. This confirms that the transition to the Iron Age was not driven by a replacement of the local population by invaders, but rather by the cultural evolution of indigenous groups.<sup>11</sup>
2. **Steppe Admixture:** In a significant departure from the Maykop pattern, Koban genomes

display a definitive signal of Steppe admixture, specifically related to Scythian populations. ADMIXTURE modeling (at K=12) reveals that while the "West Asian" (CHG/ANF) component remains dominant, a distinct "Steppe" component appears in significant proportions.<sup>13</sup> This indicates that the "semi-permeable barrier" had been breached, allowing gene flow from the Scythian nomads into the settled populations of the foothills.

3. **The Alans Connection:** Perhaps most strikingly, the genetic profile of the Koban culture is nearly identical to that of the later Alanic individuals found in the same region. This challenges the historical narrative of the Alans as a purely Iranian steppe tribe that replaced the locals. Instead, the genetic data suggests that the historical "Alans" of the North Caucasus were a genetically admixed population, likely formed by the assimilation of a Steppe elite into a populous, local Koban-derived substrate.<sup>12</sup>

**Implication for Circassians:** The Adyghe people are the linguistic and cultural heirs of the Dolmen/Meotian/Koban substrates. The genetic evidence implies that the modern Adyghe gene pool was crystallized during this Iron Age interval. The localized accumulation of Steppe ancestry into a persistent CHG/Anatolian base created the distinct genetic signature that defines the Northwest Caucasus today.

## 5. Genetic Profile of the Modern Circassians (Adyghe)

Modern Adyghe (Circassians) occupy a unique and intermediate position in the Principal Component Analysis (PCA) of West Eurasian populations. They form a genetic cline that bridges the populations of the South Caucasus (such as Georgians) and the populations of the Steppe (such as Russians and Nogais).

### 5.1 qpAdm Ancestry Modeling

Synthesizing the data from Wang et al. (2019) and the extensive "Southern Arc" dataset published by Lazaridis et al. (2022), we can construct a robust admixture model for the modern Adyghe. Utilizing qpAdm, a statistical tool that estimates ancestry proportions by comparing the test population to a set of reference "outgroups," a consensus 3-way model emerges:

- **Source 1: Caucasus Hunter-Gatherer (CHG) / Iran Neolithic: ~55–65%**
  - This is the foundational lineage, linking the Adyghe directly to the ancient Kura-Araxes and Maykop peoples. It is present at higher frequencies in the Adyghe than in any European population. However, it is slightly lower than in modern Georgians, a reduction attributable to the dilution effect of Steppe admixture in the North.<sup>14</sup>
- **Source 2: Anatolian Neolithic Farmers (ANF): ~15–20%**
  - This ancestry likely arrived via the Maykop/Darkvetsi-Meshoko horizon. While shared with Europeans (where it arrived via the Balkans), in the Caucasus, it arrived via a distinct Transcaucasian route.

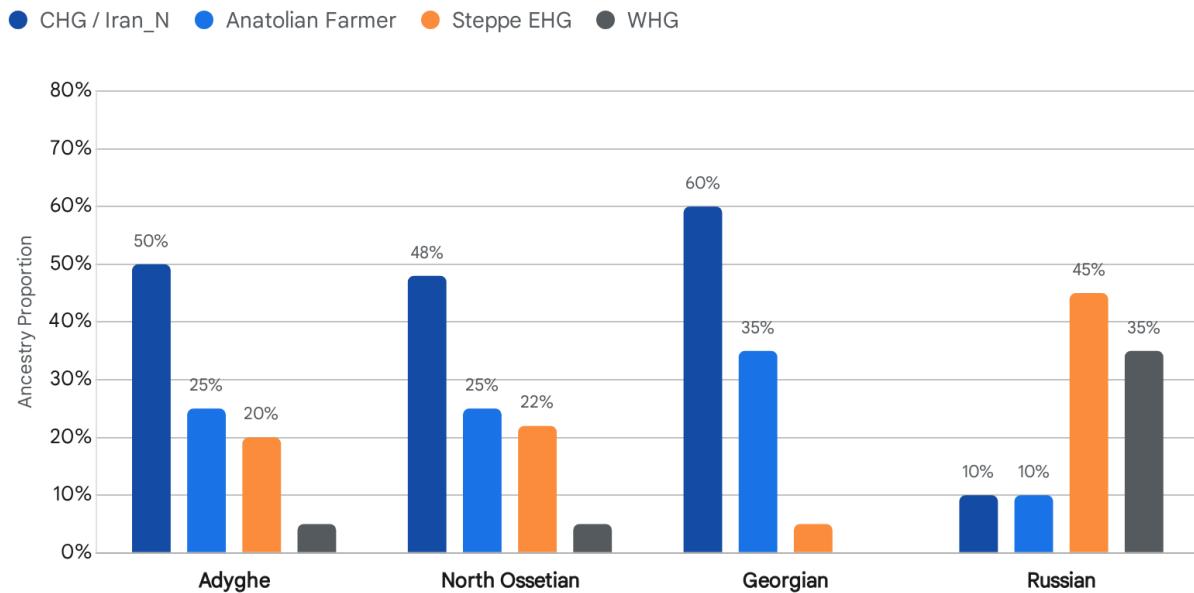
- **Source 3: Steppe / Eastern Hunter-Gatherer (EHG): ~15–25%**
  - **The Critical Differentiator:** This component represents the "leakage" across the Caucasian barrier described in Section 4. While the Early Bronze Age Maykop culture possessed less than 5% EHG ancestry, modern Adyghe harbor approximately 20%. This significant increase is the genetic legacy of the Iron Age interactions with Scythians, Sarmatians, and potentially later Turkic groups. In some models, this is represented as "Yamnaya Samara" ancestry; given that Yamnaya is roughly 50% EHG, a 40% Yamnaya score in a model translates to approximately 20% pure EHG ancestry.

## 5.2 Comparative Analysis with Neighbors

To fully contextualize the Adyghe genetic profile, it is instructive to compare it with neighboring populations using the same qpAdm framework.

- **vs. Georgians:** Georgians, particularly Western groups like the Mingrelians, model as almost pure CHG + ANF with **negligible** Steppe ancestry (typically less than 5%).<sup>7</sup> This stark contrast highlights the effectiveness of the Greater Caucasus range as a barrier; it shielded the South Caucasian populations from the Scythian influx that significantly impacted the Adyghe in the northern foothills.
- **vs. Ossetians:** North Ossetians exhibit Steppe ancestry levels that are similar to, or slightly higher than, the Adyghe. This is consistent with their linguistic origins as descendants of the Iranian-speaking Alans/Sarmatians. However, despite their linguistic shift, Ossetians remain overwhelmingly "Caucasian" (CHG) in their autosomal profile. This confirms that the Alanic impact was primarily an elite dominance event rather than a demographic replacement—the incoming Steppe Iranians imposed their language but were genetically absorbed by the local substrate.<sup>15</sup>

## Comparative Ancestry Proportions: Northwest Caucasus vs. Neighbors



Modeled ancestry proportions (qpAdm) for Adyge (Circassian), Georgian, North Ossetian, and Russian populations. Adyge and Ossetians share a similar 'North Caucasus' profile: dominant CHG/Iran\_N ancestry with moderate Steppe introgression. Georgians lack significant Steppe ancestry, while Russians are dominated by Steppe and WHG components.

Data sources: [Genome Biology and Evolution](#), [ResearchGate](#) (Nasidze et al.), [PMC](#) (Korenevskiy et al.), [Semantic Scholar](#) (Khusnutdinova et al.).

## 6. The Patrilineal Paradox: Y-Chromosome Continuity vs. Autosomal Shift

A striking feature of Northwest Caucasian genetics is the discordance between uniparental markers (specifically the Y-chromosome) and the autosomal data. This "Patrilineal Paradox" requires a reconciliation of the continuity seen in male lineages with the admixture observed in the whole genome.

### The Data:

- **Autosomal Signal:** As established, the Adyge genome contains ~15–25% Steppe ancestry.
- **Y-DNA Signal:** Adyge and Abkhaz male lineages are overwhelmingly dominated by Haplogroup **G2a** (specifically sub-clades like G-P303, G-P16, and G-L1264), often reaching frequencies of 60–70% or more.<sup>16</sup>

- **The Paradox:** In classical population genetics, Steppe ancestry is strongly correlated with the expansion of Haplogroups **R1a** and **R1b**. These lineages are dominant in Eastern Europe and are significant in Turkic groups of the Caucasus (like the Karachay-Balkars, who have high R1a frequencies). Yet, R1a and R1b are minority lineages among the Adygehe.

#### Reconciliation Models:

How did a population acquire ~20% of its genome from the Steppe without the corresponding paternal lineages replacing the indigenous ones?

1. **Female-Biased Gene Flow:** The most plausible explanation is that Steppe introgression occurred significantly through exogamy involving Steppe women. If local G2a men consistently married women from neighboring Steppe tribes (Scythians, Sarmatians) over centuries, autosomal Steppe DNA would accumulate in the population without displacing the local Y-chromosomes. This pattern is consistent with the "bride exchange" often seen in contact zones between sedentary and nomadic groups.
2. **The "Elite Dominance" Failure:** While Alanic (Sarmatian) elites clearly established political hegemony in the region—evidenced by the archaeological transition to the Alanic period and the spread of Iranian loanwords—they did not demographically replace the indigenous men. The indigenous "Colchian" or "Koban" patrilineages (G2a) survived the political stratification and eventually reasserted dominance. Alternatively, the invading Steppe elites may have been numerically small, leading their specific Y-lineages to drift out or remain as minor components (R1b-Z2103 is present but at low frequencies).
3. **Founder Effects:** The mountainous terrain of the Northwest Caucasus fosters endogamy and genetic drift. It is likely that a few successful G2a lineages experienced a massive expansion (a "star-cluster" phylogeny) during the Early Bronze Age, effectively saturating the population before the Iron Age Steppe incursions occurred. This high baseline frequency would make the G2a lineage resilient to replacement by incoming minority lineages.

## 7. Regional Context: The North vs. South Divide

Recent advancements in Identity-by-Descent (IBD) analysis, particularly highlighted in the work of **Ringbauer et al. (2024)**, have provided a higher-resolution lens for viewing the genetic history of the Caucasus. This method, which detects shared DNA segments inherited from recent common ancestors, allows for a more precise timing of admixture events than traditional allele frequency methods.

The study by Ringbauer et al. paints a picture of exceptional genetic stability in the **South Caucasus** (modern Georgia and Armenia). Spanning 5,000 years from the Early Bronze Age to the Migration Period, the South Caucasian gene pool remained remarkably constant, resisting the massive genetic turnovers that reshaped Europe during the same period. While

there was limited gene flow from the Steppe and Anatolia, the core ancestry persisted.<sup>14</sup>

In contrast, the **North Caucasus** (the Adyghe homeland) shows a divergent trajectory. While sharing the same deep CHG root, the North became a contact zone. The IBD and admixture data confirm that the "barrier" of the High Caucasus was permeable from the north but largely impermeable from the south after the Bronze Age. The North Caucasian populations acted as a buffer, absorbing Steppe migrations and preventing them from penetrating deeply into the Transcaucasian valleys. This differential history explains the current genetic structure: a North Caucasus enriched with Steppe ancestry vs. a South Caucasus that preserves a more "pristine" Near Eastern/CHG profile.<sup>19</sup>

## 8. Conclusion

The autosomal history of the Northwest Caucasus, as revealed by the latest paleogenomic research, is a testament to genetic resilience. The Circassian genome is not merely a mixture of passersby; it is a deep reservoir of Paleolithic ancestry that has successfully navigated millennia of turbulent migrations.

The trajectory can be summarized as follows:

1. **Foundation:** Laid in the Paleolithic by the Caucasus Hunter-Gatherers (CHG).
2. **Consolidation:** Solidified in the Eneolithic by the Maykop culture, which fused CHG with Anatolian ancestry to create a distinct "Caucasian" cluster that was remarkably resistant to the initial expansion of the Yamnaya steppe herders.
3. **Transformation:** The genetic barrier became permeable during the Iron Age (Koban culture), allowing Steppe ancestry to trickle into the Northern foothills. This created the distinct "North Caucasian" profile that separates the Adyghe from their Georgian neighbors.
4. **Continuity:** Despite this admixture, the core ancestry remains overwhelmingly local. The reconciliation of Y-DNA G2a dominance with moderate Steppe autosomal admixture points to a social structure where indigenous lineages maintained continuity while assimilating neighbors through complex social and marital networks.

Future research utilizing increasingly refined IBD techniques will likely further pinpoint the exact timing of these admixture events, moving beyond broad archaeological epochs to specific centuries of contact, and shedding more light on the complex social mechanisms that allowed the Adyghe identity to endure.

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