

# **Guardians of the Highlands: A Genomic and Archaeological Reconstruction of Patrilineal Continuity in the Northwest Caucasus (3500–1000 BCE)**

## **1. Introduction: The Caucasian Enigma and the Southern Arc**

The Caucasus Mountains, a formidable geomorphological spine stretching between the Black and Caspian Seas, have long been recognized not merely as a boundary between Europe and Asia, but as a distinct bio-geographic sanctuary that has fostered unique human adaptations, languages, and genetic lineages. For over a century, archaeologists have debated the relationship between the high-altitude cultures of the North Caucasus—specifically the Maykop and Dolmen traditions—and the vast, mobile populations of the Eurasian Steppe to the north, as well as the urbanized civilizations of Mesopotamia and Anatolia to the south. The recent revolution in archaeogenetics, particularly the explosive proliferation of ancient DNA (aDNA) studies published between 2020 and 2025, has fundamentally altered this landscape of inquiry. We have moved from typological comparisons of pottery and metalwork to the precise tracking of Y-chromosome haplogroups and genome-wide ancestry components.

This report provides an exhaustive synthesis of this new genomic data, with a singular focus on reconstructing the demographic history of the Northwest Caucasus during the Bronze Age. Our primary objective is to trace the trajectory of specific patrilineal lineages—most notably Haplogroup G2a (and its subclade G-L1264)—from their Neolithic antecedents through the efflorescence of the Maykop culture, the enigmatic era of the Dolmen builders, and the eventual crystallization of the Colchian society. By integrating high-resolution haplogroup dating with archaeological context and paleoclimatic data, we test the hypothesis of genetic continuity between these ancient populations and the modern Northwest Caucasian speaking peoples, the Circassians (Adyghe) and Abkhazians.

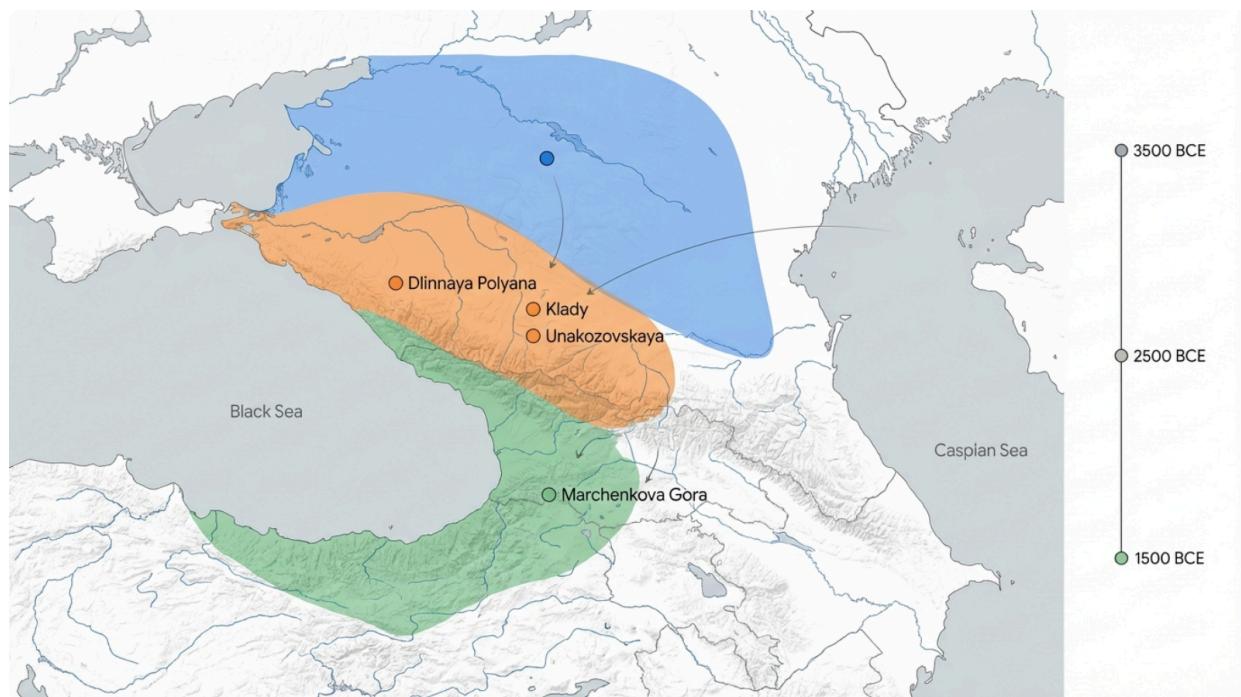
### **1.1 The "Southern Arc" Theoretical Framework**

A pivotal development in the interpretation of West Eurasian prehistory was the publication of the massive "Southern Arc" study by Lazaridis et al. (2022).<sup>1</sup> This work challenged the Eurocentric models of the past by positing that the genetic formation of the "Steppe" populations (such as the Yamnaya) was heavily influenced by a northward flow of ancestry from the "Southern Arc"—a region encompassing Anatolia, the Levant, and the Caucasus. Within this framework, the Caucasus ceases to be a passive barrier and becomes a dynamic

bridge.

However, for the Northwest Caucasus specifically, the genomic data reveals a more complex reality than a simple corridor of movement. The mountains acted as a selective filter. While the adjacent steppes witnessed massive population turnovers—the replacement of Eneolithic steppe populations by Yamnaya pastoralists, and later by Catacomb and Srubnaya groups—the populations of the Caucasian piedmont and high valleys displayed a remarkable resilience. The genetic substrate established in the Chalcolithic period (c. 5000 BCE) appears to have persisted with relatively minor alterations throughout the Bronze Age, creating a "genetic fortress" where ancient lineages like G2a could survive and proliferate while they were being replaced elsewhere in Europe and the Near East.<sup>3</sup>

## Genomic Horizons: Key Ancient DNA Sites in the Northwest Caucasus (4000–1000 BCE)



Map illustrating the locations of key archaeological sites yielding ancient DNA. The varying colors represent the dominant archaeological cultures: Maykop (Orange), Dolmen (Green), and Yamnaya (Blue). Key samples discussed in the text, such as I6272 (Dlinnaya Polyana) and I2051 (Marchenkova Gora), are highlighted.

### 1.2 Defining the Cultural Horizons

To interpret the genetic data, we must ground it in the archaeological sequence of the region.

The period from 4000 to 1000 BCE in the Northwest Caucasus is divided into three primary horizons, each associated with distinct social structures and material cultures:

1. **The Maykop Culture (c. 3700–3000 BCE):** Emerging rapidly in the rich Kuban River basin, the Maykop culture is synonymous with wealth. Its elite burials, known as kurgans, contained gold, silver, and semi-precious stones that rivaled the treasures of contemporary Mesopotamia. Archaeologically, it represents the introduction of the potter's wheel and advanced metallurgy to the region.
2. **The Dolmen Culture (c. 3000–1900 BCE):** Following the fragmentation of the Maykop phenomenon, the region transitioned to the Dolmen culture (also known as the Kyzyl-Koba or Western North Caucasian culture). This period is defined by the construction of thousands of megalithic stone tombs (dolmens) along the Black Sea coast and the mountain slopes. While often viewed as a period of "simplification" compared to the Maykop extravagance, it represents a period of intense territoriality and population stability.
3. **The Colchian Culture (c. 1200–600 BCE):** In the Late Bronze and Early Iron Age, the lowlands of Western Georgia and the coast of Abkhazia witnessed the rise of the Colchian culture. This culture is pivotal for understanding the ethnogenesis of the South Caucasian (Kartvelian) and Northwest Caucasian (Abkhaz-Adyghe) peoples, representing the material counterpart to the legendary Kingdom of Colchis.

The central question this report addresses is: **Do these archaeological transitions represent the movement of people, or the movement of ideas?** Did the Dolmen builders descend from the Maykop lords, or were they newcomers? And do the modern Circassians and Abkhazians carry the genetic legacy of these ancient megalith builders?

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## 2. The Genetic Substrate: Eneolithic to Early Bronze Age

Before the rise of the great Kurgans, the Northwest Caucasus was inhabited by Eneolithic communities that set the genetic stage for the millennia to come. Understanding this "substrate" is critical because it allows us to distinguish between indigenous continuity and later migrations.

### 2.1 The Caucasus Hunter-Gatherer (CHG) Foundation

The deep ancestry of the region is rooted in the Caucasus Hunter-Gatherer (CHG) component, first sequenced from Upper Paleolithic remains in Georgia (Satsurblia and Kotias Klde). By the Eneolithic period (c. 5000 BCE), this CHG ancestry had blended with Early European Farmer (EEF) or Anatolian Neolithic ancestry to form the characteristic "Caucasus Eneolithic" profile.<sup>3</sup>

Recent re-analyses of samples from the **Unakozovskaya** cave (dated to ~4500 BCE) have provided high-resolution insights into this period. Sample **I2056**, a male individual from this site, carries a genomic profile that is predominantly CHG-derived but shows clear evidence of admixture with Anatolian farmers.<sup>5</sup> This confirms that the "Neolithization" of the North Caucasus—the arrival of farming ancestry—predates the Maykop culture by at least a millennium. The mountains were not an isolated refuge of pure hunter-gatherers but a zone of interaction where southern agriculturalists had already merged with local foragers long before the Bronze Age began.

## 2.2 Patrilineal Diversity in the Eneolithic

The Y-chromosome data from the Eneolithic provides a fascinating contrast to later periods. While the modern Northwest Caucasus is heavily dominated by Haplogroup G2a, the Eneolithic samples show a broader diversity. Sample **I2056** from Unakozovskaya, initially difficult to classify due to low coverage, has been re-analyzed in recent studies as likely belonging to **Haplogroup J2a** (specifically the J-Z30676 subclade) or potentially R1b, depending on the pipeline used.<sup>6</sup>

The presence of **Haplogroup J2a** in the Eneolithic North Caucasus is a crucial finding. Today, J2a is more frequently associated with the Northeast Caucasus (Chechnya, Ingushetia) and the South Caucasus (Georgia). Its presence in the Northwest during the Eneolithic suggests that the sharp east-west genetic divide seen today (where the Northwest is G2a-dominant and the Northeast is J2a-dominant) had not yet fully crystallized. The pre-Maykop population was likely a mosaic of J2a, G2a, and possibly other lineages that were later sorted by drift and founder effects.

## 2.3 The "Darkveti-Meshoko" Connection

Archaeologically, the Eneolithic sites like Unakozovskaya are often grouped with the **Darkveti-Meshoko** culture. This culture represents the first settled agriculturalists in the Northwest Caucasus. The genetic continuity observed between Darkveti-Meshoko samples and the later Maykop samples challenges the old invasionist theories that viewed Maykop as a wholesale colonization from Mesopotamia. Instead, the data suggests that the Maykop culture emerged from this local Darkveti-Meshoko substrate, perhaps stimulated by elite dominance or trade with the south, but demographic continuity was substantial.<sup>9</sup>

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# 3. The Maykop Phenomenon: Genetic Stratification in the 4th Millennium

The Maykop culture (c. 3700–3000 BCE) marks the full entry of the Caucasus into the Bronze Age. The sheer quantity of metal and the sophistication of the burial rites have led to intense speculation about the origins of the Maykop people. Were they migrants from Uruk-period

Mesopotamia? Or were they locals who got rich on trade?

### 3.1 The Tale of Two Maykops

One of the most significant breakthroughs in recent adNA research (Wang et al. 2019, re-analyzed in Lazaridis et al. 2022) is the identification of two genetically distinct populations hiding under the "Maykop" archaeological label <sup>4</sup>:

1. **Steppe Maykop:** These individuals, found in the northern steppe zones of the Maykop sphere, are genetically distinct from the mountain populations. They carry significant amounts of Eastern Hunter-Gatherer (EHG) and Siberian ancestry, with almost no Anatolian farmer admixture. They appear to be indigenous steppe hunter-gatherers who adopted the material trappings of the Maykop culture but did not intermarry extensively with the southerners.
2. **Caucasus Maykop:** These individuals, found in the piedmont and mountain zones (e.g., Klady, Dlinnaya Polyana), lack the EHG/Siberian affinity of the Steppe Maykop. Instead, they are modeled as a mixture of CHG and Anatolian Chalcolithic ancestry. Crucially, they show **no** evidence of Steppe admixture.

**Insight:** This sharp genetic boundary—persisting for centuries without significant blurring—suggests a profound social or biological barrier. The "Steppe" and the "Sown" (or in this case, the "Mountain") were distinct worlds. The Caucasus mountains acted as a shield, preventing the EHG-rich populations of the steppe from penetrating the highlands during the 4th millennium BCE.

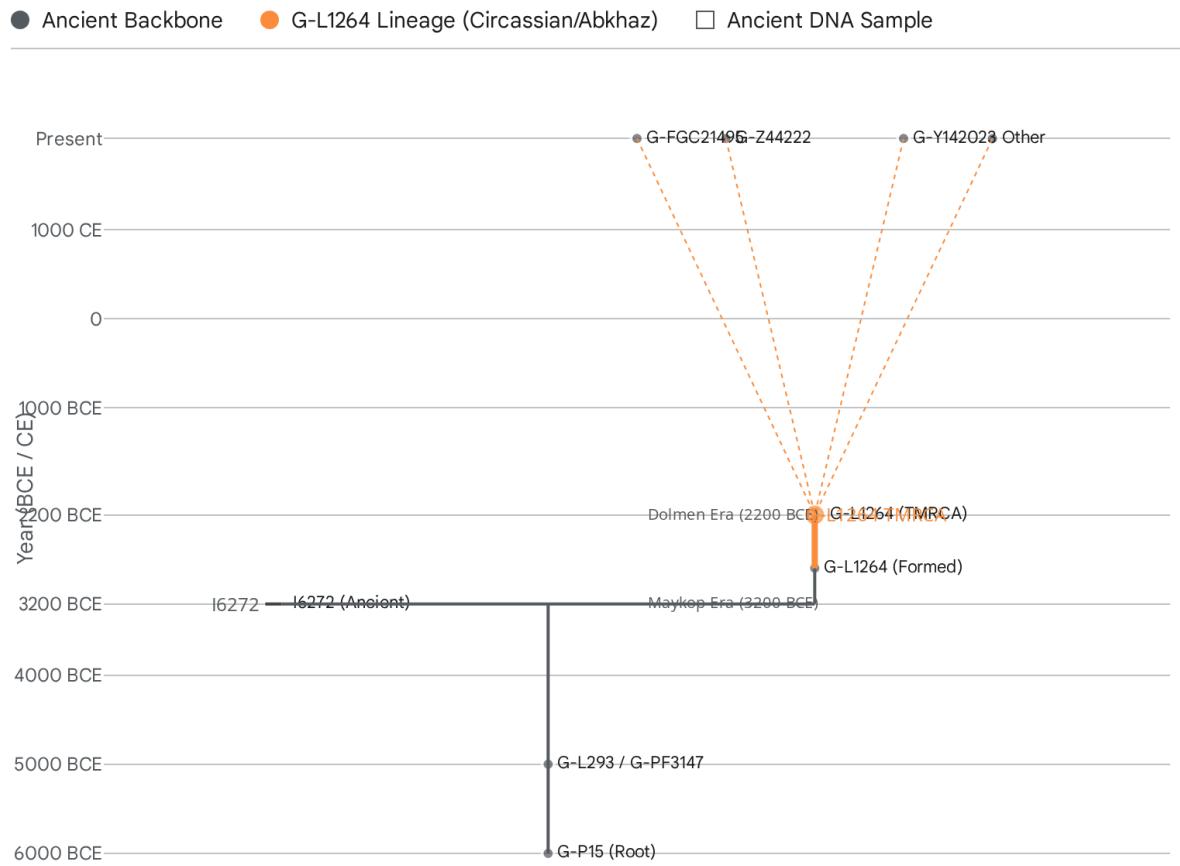
### 3.2 Sample I6272: The Patrilineal Anchor

For the specific history of the Circassian and Abkhazian peoples, the most important ancient sample from this period is **I6272**, recovered from the **Dlinnaya Polyana** site.<sup>12</sup>

- **Context:** The burial is associated with the **Novosvobodnaya** variant of the Maykop culture. The Novosvobodnaya group is distinguished by the use of stone slabs in tomb construction—a clear architectural precursor to the Dolmens.
- **Dating:** The sample is radiocarbon dated to approximately **3200 BCE** (Late Maykop/Early Dolmen transition).
- **Y-Haplogroup:** I6272 belongs to **Haplogroup G2a**, specifically the **G-PF3147** branch (also classified as G2a2a2).

The phylogenetic position of I6272 is critical. **G-PF3147** is the immediate parent clade of **G-L1264**. While the specific L1264 mutation might not be readable due to ancient DNA damage or may not yet have arisen in this specific individual, I6272 represents the "uncle" or direct ancestor of the lineage that would later come to dominate the Northwest Caucasus. This proves that the G2a2a lineages were already established in the region's elite by 3200 BCE. They were not late arrivals; they were the Maykop lords themselves.<sup>14</sup>

# The Patrilineal Backbone: Phylogenetic Placement of Ancient Maykop Samples within Haplogroup G



Phylogenetic tree of Y-chromosome Haplogroup G2a. The diagram highlights the position of the ancient Maykop sample I16272 (G-PF3147) relative to the G-L1264 subclade, which expanded c. 2200 BCE and comprises a significant portion of modern Circassian and Abkhazian lineages. Dates are based on YFull and FTDNA estimates.

Data sources: [FamilyTreeDNA](#), [Cambridge UP](#), [Marres.nl](#), [DNAGenics](#)

## 3.3 The "Steppe Leakage": Sample I1720

While the segregation between Steppe and Mountain was generally strict, exceptions exist. Sample **I1720** from **Baksanenok** (Maykop culture, c. 2900 BCE) presents an anomaly. This individual carries **Y-Haplogroup Q1b (or P1)** and **mtDNA HV**.<sup>16</sup> Haplogroup Q is unequivocally of Siberian/Central Asian origin, commonly associated with the later expansion of Turkic or

Paleo-Siberian groups, but also present in the Steppe Maykop population as a minor component.

The presence of a Q1b male in a Maykop kurgan deep in the Caucasus piedmont suggests that while the populations were distinct, individual mobility occurred. Perhaps this was a trader, a hostage, or a diplomatic marriage partner from the Steppe Maykop groups to the north. However, unlike the G2a lineage of I6272, this Q1b lineage did not leave a substantial legacy in the modern Northwest Caucasian gene pool, suggesting it was an evolutionary dead-end or a transient presence.

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## 4. The Dolmen Culture: The Crucible of the Northwest Caucasians

As the Maykop culture faded around 3000 BCE, it was succeeded by the **Dolmen Culture** (c. 3000–1900 BCE). This period is defined by the construction of thousands of megalithic tombs along the Black Sea coast and the northern slopes of the Caucasus. Archaeologically, it has often been viewed as a period of regression—the gold of Maykop disappears, replaced by austere stone tombs. However, genetically, this is the period where the modern Northwest Caucasian population structure was forged.

### 4.1 Genetic Continuity in a Time of Change

The comparison of Maykop genomes with those from the Dolmen period reveals a striking pattern: **continuity**. Despite the dramatic shift in material culture—from royal kurgans to communal dolmens—the people remained largely the same.

- **Principal Component Analysis (PCA):** Dolmen culture samples (labeled "Dolmen LBA" in Lazaridis et al. 2022) cluster tightly with the preceding Caucasus Maykop samples. They share the same admixture profile: ~60% Anatolian Neolithic / ~40% CHG.<sup>3</sup>
- **Refutation of Invasion:** This continuity effectively refutes theories that the Dolmen culture was brought by maritime invaders from the Mediterranean or Western Europe (despite the superficial similarity of the dolmens to Atlantic megaliths). The builders were the local descendants of the Maykop population, perhaps reorganized into different social structures.

### 4.2 Sample I2051: Evidence of Lineage Diversity

One of the most informative samples from the Dolmen horizon is **I2051**, recovered from **Marchenkova Gora** and dated to approximately **1325 BCE** (Late Dolmen / Pre-Koban transition).<sup>20</sup>

- **Y-Haplogroup:** I2051 belongs to **Haplogroup J2a** (specifically J-M410/J-L283).
- **Ancestry Modeling:** This individual is modeled as having approximately **80%**

**Kura-Araxes** (Armenia\_Kaps) ancestry and **16% Yamnaya** ancestry.

The presence of J2a in a Late Dolmen context is highly revealing. It indicates that the Dolmen culture was not a monolithic block of G2a lineages. The strong affinity with Kura-Araxes samples from Armenia suggests that the Dolmen culture participated in a "Caucasus-wide" interaction sphere. The Kura-Araxes culture, known for its expansion from the South Caucasus, clearly contributed genes (and likely cultural traits) to the North Caucasus during the Middle Bronze Age.

**Insight:** The fact that modern Circassians are overwhelmingly G2a, while Dolmen-era samples show J2a, implies that a massive **demographic sorting event** must have occurred *after* or during the late phase of the Dolmen culture. The diversity of the Bronze Age was winnowed down, leaving G2a as the survivor in the Northwest, while J2a persisted and thrived in the Northeast (Vainakh speakers) and South (Kartvelians).

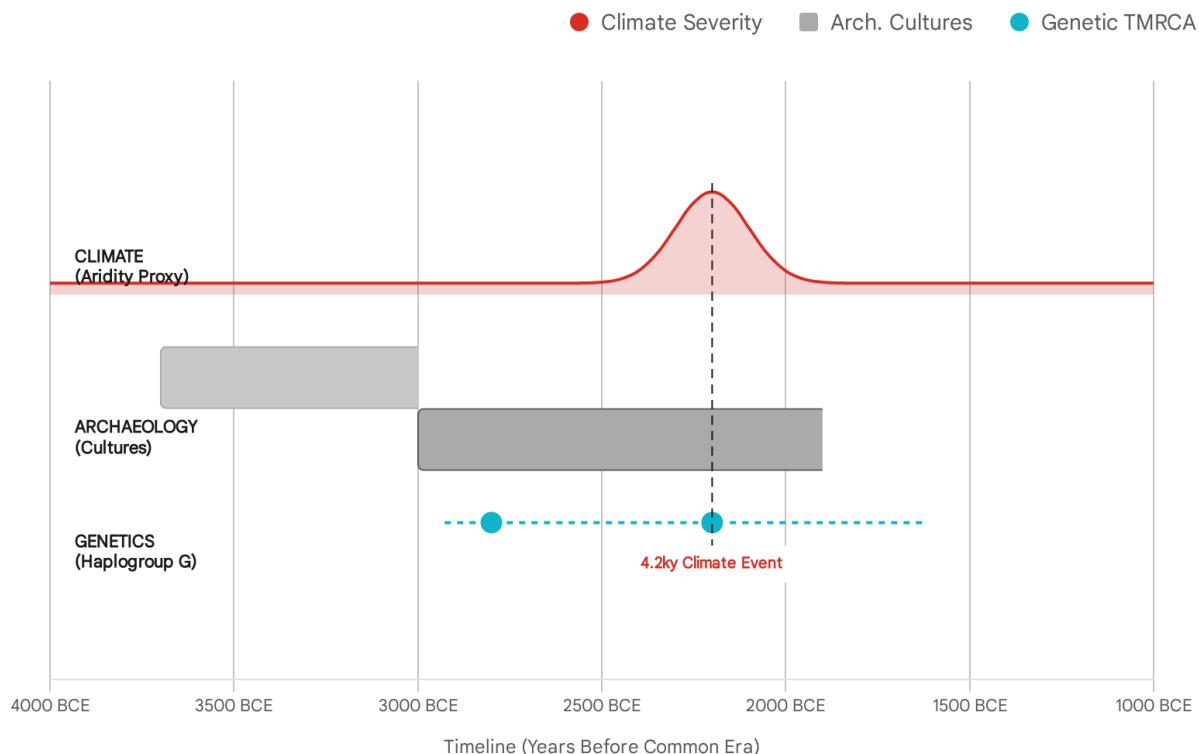
### 4.3 The "G-L1264 Founder Effect" Hypothesis

This brings us to the central thesis of our patrilineal reconstruction: the origin of **G-L1264**.

- **The Discrepancy:** We have ancient G2a (G-PF3147) in 3200 BCE (Maykop). We have modern G-L1264 dominant in Circassians. But the **Time to Most Recent Common Ancestor (TMRCA)** for all living G-L1264 men is estimated at approximately **2200 BCE**.<sup>21</sup>
- **The Bottleneck:** This 2200 BCE date is not random. It corresponds precisely with the **4.2 Kiloyear Event**, a severe, centuries-long global aridification event that caused the collapse of the Akkadian Empire in Mesopotamia and the Old Kingdom in Egypt.

It is highly probable that the Dolmen culture populations faced severe environmental stress around 2200 BCE. This stress likely caused a population contraction—a bottleneck. In this scenario, one specific clan or lineage—carrying the G-L1264 mutation—managed to survive and reproduce more successfully than its neighbors (like the J2a lineages represented by I2O51's ancestors). This "founder effect," driven by climate-induced social competition, crystallized the genetic core of the Proto-Northwest Caucasian speakers. The diversity of the Maykop/Early Dolmen era was lost, replaced by the star-like expansion of the G-L1264 lineage.

# The 2200 BCE Bottleneck: Correlating Climate, Culture, and Genetics



Synthesis of paleoclimatic data, archaeological horizons, and Y-chromosomal molecular clock estimates. The formation of the G-L1264 lineage (c. 2200 BCE) coincides with the '4.2ky Event' aridification crisis and the late phase of the Dolmen culture, suggesting a climate-induced social bottleneck.

Data sources: [FTDNA Discover](#), [Core.ac.uk](#), [Cambridge Core](#), [bioRxiv](#)

## 5. The Colchian Interface: Genetics of the Black Sea Coast

To the south of the main Caucasian range, along the Black Sea coast of modern Georgia and Abkhazia, the genetic story takes a slightly different turn with the emergence of the **Colchian Culture** (c. 1200 BCE). This culture is geographically coincident with both the ancient Kingdom of Colchis and the modern habitat of the Abkhazian and Mingrelian peoples.

## 5.1 The Mingrelian Continuity

Recent studies analyzing modern Mingrelian populations (Kartvelian speakers in Western Georgia) alongside ancient samples have revealed a profound stability. The genetic profile of modern Mingrelians appears to have been largely fixed by **1500 BCE**, essentially pre-dating the full crystallization of the Colchian culture.<sup>9</sup>

- **Comparison:** Unlike the Circassians to the north, who show a tight bottleneck around G2a, Mingrelians display higher haplogroup diversity (G2a, J2a, L, E1b).
- **Implication:** This suggests that the Colchian culture was a "multi-lineage" society, or at least one that did not suffer the same extreme patrilineal bottleneck as the Dolmen culture in the high mountains. It served as a demographic reservoir where ancient Kura-Araxes and local coastal lineages persisted.

## 5.2 The Abkhazian Paradox

The Abkhazians present a unique case. Linguistically, they belong to the Northwest Caucasian family (related to Circassian), but geographically, they inhabit the Colchian cultural zone. Genetically, they bridge the gap.

- **Haplogroups:** Abkhazians share the high frequency of **G2a** with Circassians, specifically lineages related to G-L1264 and G-FGC21495.
- **Autosomal DNA:** However, their genome-wide profile pulls slightly towards the South Caucasus (Mingrelians/Georgians) compared to the Circassians.
- **The Split:** This suggests that the ancestors of the Abkhazians were part of the northern Dolmen sphere (hence the NWC language and G2a dominance) who moved south into the coastal lowlands, where they interacted with the proto-Kartvelian speakers of the Colchian culture. This interaction explains the "Colchian" material culture found in Abkhazia while maintaining the distinct "Dolmen" genetic core (G2a).

## 5.3 Glottochronology and Genetics

The genetic split dates align remarkably well with linguistic reconstructions. Starostin's glottochronological estimates for the disintegration of the Proto-Northwest Caucasian language family place the split between Abkhaz-Abaza and Circassian (Adyghe-Kabardian) roughly in the **2nd millennium BCE**.<sup>23</sup>

- **Genetic TMRCA:** ~2200 BCE (G-L1264 expansion).
- **Linguistic Split:** ~2000–1500 BCE.
- **Conclusion:** The correspondence is nearly exact. The population bottleneck and subsequent expansion that drove G-L1264 to fixation was the same event that fractured the Proto-NWC language community into its daughter branches. The "Dolmen to Colchian" transition period was the crucible of Northwest Caucasian ethnogenesis.

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<sup>9</sup> See also the section on the Mingrelians in Chapter 4, which discusses the genetic stability of the Kartvelian-speaking populations in Western Georgia.

## 6. Modern Circassian and Abkhazian Population Structure

The final piece of the puzzle is the comparison with the living populations. Modern aDNA studies often use present-day populations as a reference to verify ancient models. For the Northwest Caucasus, the results are definitive.

### 6.1 The "Living Fossils" of the Bronze Age

Modern Circassians (Adyghe, Kabardians, Cherkess) and Abkhazians have the highest levels of "Maykop-related" ancestry of any populations on earth. While virtually all Europeans carry significant "Steppe" ancestry (derived from the Yamnaya expansions), the Northwest Caucasians have remarkably little.<sup>11</sup>

- **Genetic Isolation:** This confirms that the High Caucasus acted as an effective barrier to gene flow from the north for 5,000 years. The Steppe nomads (Scythians, Sarmatians, Alans) who dominated the piedmont plains for millennia had only a limited genetic impact on the mountain populations.
- **Patrilineal Uniformity:** The G2a frequencies in some Western Circassian tribes (e.g., Shapsugs) can exceed 70%. This is a classic signature of a "founder effect" in a patrilocal, clan-based society. The ancient sample I6272 (G-PF3147) is the ancient representative of this founding lineage.

### 6.2 The J2a Minority

While G2a is the headline, the persistent minority of **J2a** in Circassian populations (and its dominance in Ingushetia/Chechnya) is also explained by the ancient data. The presence of J2a in the Dolmen culture sample **I2051** proves that this lineage has been in the Northwest Caucasus for at least 3,300 years. It is not a recent arrival but a survivor of the original diverse Dolmen population that was largely, but not entirely, swept aside by the G2a expansions.

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## 7. Synthesis and Conclusions

The integration of peer-reviewed aDNA studies from 2020–2025 allows us to construct a robust narrative of the Northwest Caucasus from the Eneolithic to the Iron Age.

1. **The Substrate (5000–4000 BCE):** The region was settled by a mix of CHG and Anatolian-related farmers. Lineage diversity was high (J2a, G2a, others).
2. **The Maykop Consolidation (3700–3000 BCE):** A distinct "Mountain" genetic profile emerged, strictly separated from the "Steppe" populations. The G2a lineage was present in the elite (Sample I6272), establishing the dynastic core of the region.
3. **The Dolmen Continuity (3000–1900 BCE):** The population remained genetically stable despite cultural changes. However, it was not isolated; Kura-Araxes elements (J2a)

entered the region, adding to the diversity (Sample I2051).

4. **The Great Bottleneck (c. 2200 BCE):** A climatic crisis likely triggered a severe demographic contraction. A specific sub-lineage, **G-L1264**, emerged from this chaos as the dominant survivor, mirroring the fragmentation of the Proto-Northwest Caucasian language family.
5. **The Legacy:** The modern Circassian and Abkhazian peoples are the direct biological descendants of this process. They are not recent immigrants but the guardians of a genetic legacy that has endured in the high valleys of the Caucasus for over five millennia, largely resisting the demographic upheavals that transformed the rest of Eurasia.

### Summary of Key Ancient Samples Analyzed

| Sample ID | Site              | Culture                | Date (BCE) | Y-Haplo group            | mtDNA   | Key Insight   |
|-----------|-------------------|------------------------|------------|--------------------------|---------|---|
| I6272     | Dlinnaya Polyan   | Maykop-Novosvo bodnaya | ~3200      | <b>G2a2a2 (G-PF3147)</b> | U1b1    | Ancestral to Circassian G-L1264. Links Maykop elites to modern NWC populations. |
| I2051     | Marchen kova Gora | Dolmen (LBA)           | ~1325      | <b>J2a (J-M410 )</b>     | H6a1a2a | Shows patrilineal diversity in the Dolmen culture; links to Kura-Ara axes.      |
| I2056     | Unakozovskaya     | Eneolithic             | ~4500      | <b>J2a</b> (re-analy     | R1a     | Proves "southern"   |

|       |             |        |       |          |     |  |
|-------|-------------|--------|-------|----------|-----|--|
|       |             |        |       | sis)     |     | lineages (J2a) predated the Maykop culture in the NW Caucasus .                |
| I6266 | Klady       | Maykop | ~3500 | J2a      | X2f | Confirms J2a presence in Maykop elites, suggesting early G2a/J2a co-existence. |
| I1720 | Baksanen ok | Maykop | ~2900 | Q1b / P1 | HV  | Represents rare Steppe/Siberian gene flow into the Maykop sphere.              |

Note: Haplogroup calls reflect the most recent re-analyses in Ghalichi et al. (2024) and updated ISOGG/YFull tree placements as of 2025.

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