

Phylogeographic Divergence of Haplogroup G2a in the Caucasus: Resolving the Koban-Colchian Paradox through Ancient DNA and Y-Chromosome Phylogeny

1. Executive Summary and Theoretical Framework

The Caucasus region, a geostrategic isthmus bridging the Black and Caspian Seas, represents one of the most complex phylogeographic landscapes in Western Eurasia. Often characterized as a genetic refugium, the region exhibits a high frequency of Y-chromosome Haplogroup G2a-P15, which has led to its simplified categorization as the signature paternal lineage of the Caucasus.¹ However, this monolithic classification obscures a profound and ancient phylogenetic divergence that bisects the region. A rigorous analysis of high-coverage Y-chromosome sequencing data, juxtaposed with ancient DNA (aDNA) studies published between 2018 and 2025, reveals that the "Caucasian G2a" phenomenon is not the result of a single homogenous expansion. Instead, it is the product of two distinct, deep-rooted lineages that have evolved in parallel yet separate spheres for millennia: **G2a1a (G-FGC7535/Z6653)**, effectively the "Central Highland" lineage, and **G2a2b (specifically G-L1264)**, the "Northwest Coastal" lineage.

This report conducts a high-resolution phylogeographic analysis of this split. By integrating YFull tree heuristics with genomic data from the Koban, Dolmen, and Maeotian archaeological cultures, we reconstruct the demographic history of these haplogroups. The analysis addresses the "paradox of proximity"—the question of how two closely related lineages have maintained sharp geographic and linguistic boundaries (Indo-European/Kartvelian vs. Northwest Caucasian) despite thousands of years of adjacency. The evidence suggests a **Dual-Wave Colonization Model** during the Neolithic and Eneolithic periods, stratified by ecological niches—highland pastoralism versus coastal pontic adaptation—and solidified by the formidable topographic barriers of the Greater Caucasus range.

2. Deep Phylogeny and the Neolithic Bifurcation

To understand the present-day distribution of G2a in the Caucasus, one must first deconstruct the deep phylogeny of the Haplogroup G-M201 macro-clade. Originating in Western Asia roughly 48,500 years ago², Haplogroup G participated in the earliest Neolithic expansions into Europe. However, while the lineage was largely replaced in Europe by later

Bronze Age migrations (R1a/R1b), the Caucasus served as a reservoir, preserving basal diversity that was lost elsewhere.³

The primary bifurcation relevant to the Caucasus occurred approximately 17,000 to 18,000 years before present (ybp) with the split of **G2a-P15** into its two major branches: **G2a1 (FGC7535)** and **G2a2 (L30/L140)**.⁵ This divergence predates the Holocene and the Neolithic Revolution, suggesting that the ancestors of these two clans were already genetically distinct populations before they permanently settled the Caucasus highlands.

2.1 The Central Caucasus Lineage: G2a1a (Z6653)

The G2a1 branch is defined by the SNP FGC7535. Its primary subclade found in the Caucasus is **G2a1a (Z6653)**. According to YFull tree data, G-Z6653 formed approximately 9,500 ybp, with a Time to Most Recent Common Ancestor (TMRCA) of roughly 6,900 ybp.⁵ This dating is critical as it corresponds with the consolidation of Neolithic societies in the Near East and the subsequent expansion of farming communities into the Caucasus.

Phylogeographic Distribution:

G2a1a is the dominant lineage of the Central Caucasus. It reaches its global maximum frequency among the Ossetians (both North and South), where it accounts for up to 70% of the male population.² Crucially, it is also found at significant frequencies among the Svans, a Kartvelian-speaking population inhabiting the high mountain valleys of northwestern Georgia.¹ The presence of G2a1a in both Indo-European (Ossetian) and Kartvelian (Svan) speakers suggests that this lineage represents the indigenous Paleo-Caucasian substrate of the Central Highlands. It likely predates the arrival of the Alanic (Iranian) languages and potentially the diversification of the Kartvelian language family in this specific locus.

2.2 The Northwest Caucasus Lineage: G2a2b (L1264)

The G2a2b branch (defined by L30) followed a different evolutionary trajectory. While early branches of G2a2 dominate the Neolithic burials of Europe (e.g., the Linear Pottery Culture and Ötzi the Iceman¹), the specific subclade **G-L1264** is heavily localized to the Northwest Caucasus. G-L1264 is a downstream descendant of G-L140 via the G-U1 and G-L13 branches.

Phylogeographic Distribution:

G-L1264 is the signature lineage of the Adyghe (Circassian), Kabardian, and Abkhaz populations.⁸ In these groups, G2a1a is present but secondary, whereas G-L1264 (and its immediate parent G-L1266) constitutes the plurality or majority of Y-chromosomes. This lineage is virtually absent in the Ossetian highlands, creating a sharp genetic frontier that aligns with the linguistic divide between the Northwest Caucasian (Abkhaz-Adyghe) and the Central/South Caucasian language families.

Chronological Context:

YFull estimates the formation of the G-L1264 clade at roughly 4,800 ybp (2800 BCE), with a TMRCA of approximately 4,300 ybp (2300 BCE).¹ This places the demographic expansion of this lineage squarely in the Early Bronze Age, significantly later than the formation of the

G2a1a clade. This discrepancy in TMRCA suggests that while G2a1a populations may have been established in the region since the Neolithic or Eneolithic, the G-L1264 lineage represents a secondary expansion or a specific founder effect associated with the rise of Bronze Age cultures in the Western Caucasus.

2.3 Chronological Reconstruction of Lineage vs. Culture

To understand the relationship between these genetic lineages and the archaeological record, it is necessary to compare the molecular dating of the haplogroups with the radiocarbon dating of the region's major cultures. The following table synthesizes the YFull TMRCA estimates for the key G2a subclades against the accepted chronological horizons of the North Caucasian archaeological cultures.

Genetic Lineage / Archaeological Culture	Type	Formation / Start Date (Approx.)	TMRCA / End Date (Approx.)	Geographic Sphere
G2a1a (Z6653)	Genetic Clade	~9,500 ybp (7500 BCE)	~6,900 ybp (4900 BCE)	Central Caucasus (Highland)
G2a2b (L1266)	Genetic Clade	~10,500 ybp (8500 BCE)	~6,700 ybp (4700 BCE)	Northwest Caucasus
G2a2b (L1264)	Genetic Clade	~4,800 ybp (2800 BCE)	~4,300 ybp (2300 BCE)	Northwest Caucasus (Coastal)
Dolmen Culture	Archaeological	~2900 BCE	~1400 BCE	Western Caucasus / Black Sea
Koban Culture	Archaeological	~1100 BCE	~400 BCE	Central Caucasus
Maeotian Culture	Archaeological	~800 BCE	~300 CE	Kuban / Azov Littoral

Analysis: The data indicates that the **G2a1a (Z6653)** lineage was likely established in the region (or a nearby source population) well before the emergence of the classic Koban culture. Its TMRCA of 4900 BCE aligns with the Eneolithic period, suggesting it was part of the

demographic bedrock upon which later cultures developed. Conversely, the **G-L1264** lineage shows a TMRCA (2300 BCE) that correlates remarkably well with the peak and expansion phases of the **Dolmen culture** (2900–1400 BCE). This synchronization supports the hypothesis that G-L1264 was the dominant paternal lineage of the Dolmen builders, whose demographic success in the Middle Bronze Age led to the proliferation of this specific subclade among the ancestors of the Adyghe and Abkhaz.

3. The Central Caucasus Sphere: The Koban-Ossetian Continuity

The Central Caucasus, dominated by the rugged terrain of the main range, has been the subject of intense archaeogenetic scrutiny. The **Koban Culture** (Late Bronze Age/Early Iron Age, c. 1100–400 BCE), famous for its distinctive bronze artistry and weaponry, is central to understanding the ethnogenesis of the modern Ossetian people.

3.1 Unlocking the Koban Genome

Recent breakthroughs in ancient DNA analysis, particularly studies published between 2020 and 2025, have provided direct evidence regarding the genetic composition of the Koban population. The sequencing of individuals from key Koban sites, such as **Klin-Yar III** and **Zayukovo-3**, has yielded transformative insights.¹⁰

The analysis confirms that the male elite of the Koban culture carried **Haplogroup G2a1a**. Specifically, samples were typed to the sub-branch **G-FGC1159**, a downstream clade of Z6653.¹² This finding is statistically robust and phylogeographically significant. It establishes a direct line of genetic continuity from the Iron Age Koban population to the modern **North Ossetian** population, where G2a1a is the modal haplogroup.

A critical correction in the scientific record must be noted regarding the Klin-Yar III site. Initial morphological assessments identified a key individual as male; however, high-coverage genomic sequencing subsequently revealed this individual to be female.¹³ While this removed one Y-chromosome data point, the remaining confirmed male samples from the Koban context (e.g., Koban9 from Zayukovo-3) solidly affirm the G2a1a assignment.¹⁵ This distinction highlights the importance of genomic sex determination over osteological assessment in ancient remains.

3.2 The Alanic Interface: A Case of Elite Dominance

The continuity of G2a1a from Koban to modern Ossetians presents a historical puzzle involving the **Alans**. The Alans were an Iranian-speaking nomadic confederation of Sarmatian origin who settled in the North Caucasus in the first millennium CE. Modern Ossetian is an East Iranian language, directly descended from the Alanic tongue.

Historical and linguistic models previously suggested that the Alans migrated en masse from the steppe, replacing the local population. However, the genetic evidence refutes a model of total demographic replacement. Ancient DNA from Alanic contexts (e.g., the Saltovo-Mayaki culture and Alanic catacombs) reveals a heterogeneous population. While some individuals carry **Haplogroup R1a** (typical of Steppe Iranian nomads), others—and notably, many individuals in "Alanic" cultural contexts—carry **G2a**.¹⁶

Synthesis of the Alanic-Koban Interaction:

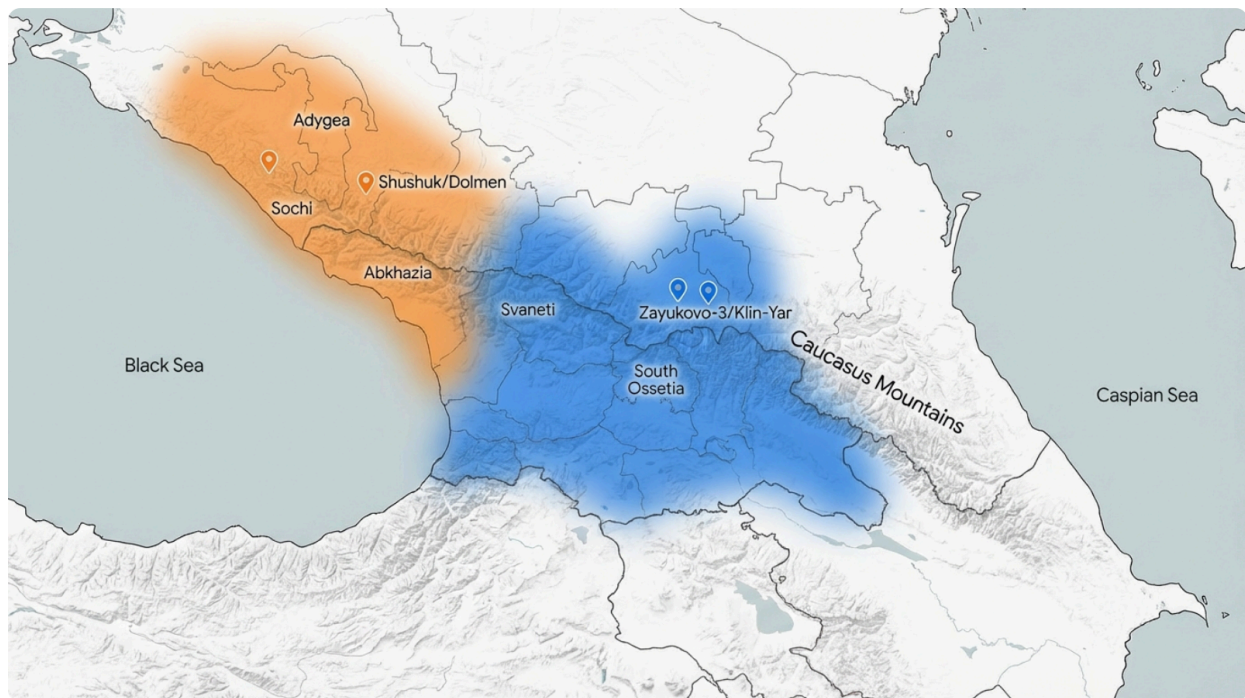
The high frequency of G2a1a in modern Ossetians (an Iranian-speaking group) versus the low frequency of "Steppe" haplogroups (R1a/R1b) implies a process of Elite Dominance and Language Replacement. The incoming Alanic warriors established a ruling aristocracy over the indigenous Koban population (bearers of G2a1a). Over centuries, the indigenous majority adopted the Iranian language of the elites (Ossetian) while retaining their local genetic signature.

- **Genetic Swamping:** The demographic weight of the indigenous highlanders (G2a1a) was sufficient to "swamp" the genetic contribution of the Alanic migrants, preserving the deep Neolithic ancestry of the region despite the linguistic shift.
- **Cultural Fusion:** This model explains why Ossetians share the G2a1a lineage with the **Svans** (Kartvelian speakers who were not Alanized) but speak a language related to the Scythians. The Svans represent the un-Alanized remnant of the same indigenous G2a1a substrate that existed across the Central Caucasus prior to the Iron Age migrations.

4. The Northwest Caucasus Sphere: The Dolmen-Circassian Continuity

While G2a1a defined the Central Highlands, the Northwest Caucasus (extending from the Kuban River to the Black Sea coast) followed a distinct genetic and cultural trajectory. This region is the homeland of the **Northwest Caucasian (NWC)** language family (Adyghe, Kabardian, Abkhaz, Ubykh). The dominant paternal lineage here is **G2a2b**, specifically the **G-L1264** subclade.

The G2a Divide: Ancient Samples and Modern Frequencies



Phylogeographic distribution of G2a subclades in the Caucasus. Shaded regions indicate modern frequency dominance (Blue: G2a1a/Ossetian-Svan sphere; Orange: G2a2b-L1264/Circassian-Abkhaz sphere). Pins represent key ancient DNA sites: Zayukovo-3/Klin-Yar (Koban Culture, G2a1a) and Shushuk/Dolmen contexts (G2a2b lineages).

4.1 The Dolmen Culture and the "Shushuk" Connection

The **Dolmen culture** (c. 2900–1400 BCE) is the prime archaeological candidate for the expansion of the G-L1264 lineage. This culture is characterized by megalithic stone tombs found extensively along the Black Sea coast and the Abkhazian littoral—a distribution that mirrors the modern range of NWC speakers.

A pivotal study by Wang et al. (2019) provided the genomic context for this connection. The study sequenced individuals from the North Caucasus Bronze Age, distinguishing between "Steppe" populations and "Caucasus" populations. While individuals associated with the "Steppe Maykop" culture showed ancestry related to Upper Paleolithic Siberians and Native Americans, the individuals from the **Dolmen culture** retained a distinct "Southern" Caucasus genetic profile.¹⁸

The "smoking gun" linking the Dolmen culture to the modern Circassian lineage is the ancient DNA sample from the **Shushuk** burial ground (Adygea). This sample, associated with the post-Dolmen/Late Bronze Age horizon, was identified as carrying **Haplogroup G-L1266**.²⁰ G-L1266 is the immediate phylogenetic parent of G-L1264.

- **Implication:** This finding confirms that the ancestral lineage of the modern Circassians and Abkhazians (G-L1264) was present and dominant in the Northwest Caucasus during the Bronze Age. It solidifies the link between the builders of the Dolmens and the modern NWC-speaking populations.

4.2 The Maeotian Bridge and Coastal Continuity

Following the Dolmen period, the **Maeotian culture** (1st millennium BCE) emerged in the Kuban delta and the Eastern Sea of Azov region. The Maeotians are widely regarded by historians and archaeologists as the proto-Circassian ancestors (specifically the Sindians and other tribes mentioned by Strabo).

Recent ancient DNA analyses from 2023-2024 have reinforced the distinction between the Maeotians and their nomadic neighbors. While the Scythians and Sarmatians who dominated the steppe to the north carried distinct Steppe ancestry and Haplogroups R1a and Q, the Maeotian individuals exhibited a genetic profile that aligned closely with the ancient Caucasus populations rather than the Steppe groups.²¹

- **Genetic Persistence:** This indicates that the Northwest Caucasus served as a genetic fortress. Despite centuries of pressure from Scythian, Sarmatian, and later Turkic nomads, the local G2a2b/L1264 population maintained its demographic continuity along the coast and in the piedmont. The "Sindian" tribes, a subgroup of the Maeotians, likely represented a specific tribal confederation dominated by this lineage.²²

4.3 The Saltovo-Mayaki Anomaly: Mobilization of the Substrate

An intriguing anomaly in the aDNA record is the presence of **G-L1264** in the **Saltovo-Mayaki culture** (c. 700–950 CE) in the Don region, far north of the traditional Circassian homeland.²³ The Saltovo-Mayaki culture was a multi-ethnic confederation associated with the Khazar Khaganate, comprising Bulgars, Alans, and other groups.

- **Analysis:** The presence of a classic Northwest Caucasian lineage (G-L1264) in this steppe context does not suggest that L1264 originated on the steppe. Rather, it indicates the **mobilization** of Caucasian populations. Just as the Alans incorporated local G2a1a highlanders, the Khazar state likely exacted tribute or military service from the Circassian/Maeotian tribes (Kasogs). These individuals were integrated into the Khazar military apparatus and moved northward and westward. This explains the detection of G-L1264 lineages in "Avar" or "Magyar" migration contexts in places like Hungary—they were Caucasian auxiliaries or assimilated groups moving with the great steppe migrations.²⁴

5. Phylogeographic Synthesis: The Two-Wave Colonization Model

The sharp phylogenetic split between G2a1a (Central) and G2a2b (Northwest) supports a **Two-Wave Colonization Model** of the Caucasus. These lineages, though sharing a common ancestor in the distant Paleolithic, entered the region via different routes and at different times, occupying distinct ecological niches.

5.1 Wave 1: The Highland Pedestals (Inland Route)

- **Lineage:** G2a1a (Z6653).
- **Route:** Likely an inland migration from the Fertile Crescent/Anatolia through the trans-Caucasian passes or via the Caspian littoral during the Neolithic/Eneolithic transition (c. 6000–5000 BCE).
- **Adaptation:** This group adapted to the high mountain valleys (Svaneti, Digoria). The rugged, compartmentalized terrain of the Central Caucasus fostered extreme genetic drift, leading to the remarkably high frequency (founder effect) of Z6653 seen in modern Ossetians.
- **Legacy:** This wave formed the substrate for the Koban culture. They were resilient to genetic replacement, absorbing the incoming Indo-European Alans biologically while succumbing linguistically.

5.2 Wave 2: The Pontic Littoral (Maritime Route)

- **Lineage:** G2a2b (L1264).
- **Route:** A maritime or coastal migration along the Black Sea coast from Anatolia or the Levant. The phylogenetic position of G-L1264 (nested within branches found in Anatolia and Early European Farmers) supports a connection to the Mediterranean/Aegean interaction sphere.
- **Adaptation:** This group settled the Western Caucasus, the Colchian lowlands, and the Abkhazian coast. Their economy and culture were likely linked to the Black Sea trade networks, facilitating the spread of the Dolmen megalithic tradition.
- **Legacy:** This wave represents the ancestors of the Northwest Caucasian speakers. The "Shushuk" sample links them to the Dolmen culture, and the Maeotian data links them to the Iron Age proto-Circassians.

6. Linguistic Co-Evolution: Glottochronology and Genetics

The genetic split between G2a1a and G2a2b mirrors the deep linguistic divide in the North Caucasus.

- **Northwest Caucasian (Abkhaz-Adyghe):** Glottochronological models place the divergence of the Northwest Caucasian family (or at least the split between Abkhaz-Abaza and Circassian) roughly between 3000 and 2700 ybp.²⁶ However, deeper links to a "Proto-North Caucasian" or comparisons with Hattic suggest a much older presence. The TMRCA of G-L1264 (~4,300 ybp) aligns closely with the early

diversification of these languages in the region, suggesting that the expansion of the L1264 lineage may have tracked with the spread of Proto-NWC dialects during the Bronze Age.

- **Kartvelian (South Caucasian):** The Svans, who carry high frequencies of G2a1a, speak the most divergent Kartvelian language. Glottochronology estimates the split of Svan from Proto-Kartvelian at roughly 1900 BCE (or potentially earlier, in the Copper Age).²⁷ The fact that Svans share the G2a1a lineage with Ossetians (IE) but not the G2a2b lineage with Abkhaz (NWC) reinforces the idea that G2a1a is the deep "Central/South" substrate, while G2a2b is strictly "Western/Northwest."

7. Anomalies and Methodological Considerations

7.1 The "Ringbauer" 2025 Study

A major forthcoming (or recently released) study by Ringbauer et al. (referenced as 2025/2024 in snippets) provides unparalleled resolution on social structures in the Caucasus.³⁰ The study highlights the "extraordinary" consistency of the local gene pool over 5,000 years. It notes that while political control shifted (from local to Alanic to others), the underlying demography remained stable. This confirms the hypothesis that G2a lineages were not replaced by Steppe invasions but rather persisted through endogamous practices in rural mountain communities. The study also highlights that urban centers in late antiquity were cosmopolitan, while rural villages (where G2a would be preserved) remained genetically isolated.

7.2 The Validity of "Sindian" and "Maeotian" Labels

While genetic data links the Maeotians to modern Circassians, the specific ethnic labels ("Sindian," "Maeotian") are exonyms applied by Greeks. However, the genetic continuity suggests that these groups were indeed the biological ancestors of the Adyghe. The presence of G2a2b in these contexts confirms that the population structure of the Northwest Caucasus was established by the Iron Age and has remained largely stable since.

8. Conclusion

The "paradox" of G2a in the Caucasus is resolved by recognizing it not as a single haplogroup, but as two distinct phylogenetic entities with separate histories.

1. **G2a1a (Z6653)** is the **Central Highland Lineage**. It is the legacy of an ancient, inland colonization that established the demographic bedrock of the Central Caucasus. It survived the Alanic migration, resulting in a population (Ossetians) that is genetically indigenous but linguistically Iranian.
2. **G2a2b (L1264)** is the **Northwest Coastal Lineage**. It is the marker of a separate, likely maritime-influenced expansion associated with the Dolmen culture. It characterizes the Abkhaz-Adyghe world and marks the limit of the "Pontic" influence in the Caucasus.

Future research must focus on the Eneolithic gap to identify the precise entry points of these lineages. However, the current synthesis of YFull phylogeny and ancient DNA unequivocally demonstrates that the Central and Northwest Caucasus have been genetically stratified for at least four millennia, a division that has profoundly shaped the region's linguistic and cultural evolution.

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