

The Sentinel of the Heights: Genomic Continuity, Patrilineal Founder Effects, and the G2a1a Paradox in the Svan Population of the Southern Caucasus

1. Introduction: The Highland Isolates of the Caucasus

The Greater Caucasus mountain range, a formidable geological barrier stretching 1,200 kilometers between the Black and Caspian Seas, has long been recognized by anthropologists and geneticists as a "refugium"—a sanctuary where ancient biological and cultural diversity has been preserved against the homogenizing sweep of steppe migrations, imperial expansions, and globalization. Within this rugged landscape, the Svan population of northwestern Georgia occupies a unique and scientifically critical position. Inhabiting the sequestered, high-altitude valleys of the Enguri and Tskhenistskali rivers—often referred to as the "roof of Europe"—the Svans have maintained a distinct ethnolinguistic identity for nearly four millennia.

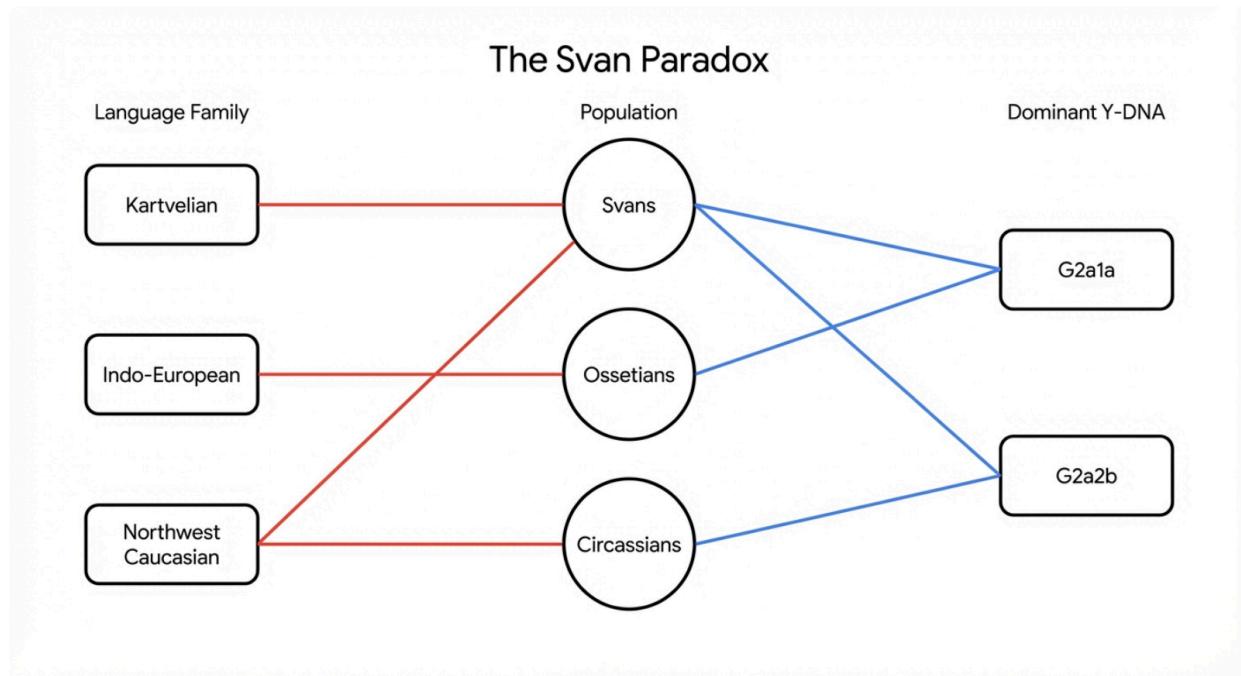
The Svan language (*Lushnu*) is the most divergent branch of the Kartvelian (South Caucasian) language family, having split from the Proto-Kartvelian common ancestor approximately 3,900 to 4,000 years ago.¹ This profound linguistic separation, predating the divergence of Georgian and Mingrelian (Zan) by nearly two millennia, suggests a history of deep isolation. One might expect such a population to serve as a genetic reservoir for the proto-Kartvelian signature. However, the advent of high-resolution archaeogenetics has illuminated a striking and counterintuitive reality: a phenomenon we designate as the "G2a1a Paradox."

While linguistically Kartvelian, the Svan paternal gene pool is not merely a subset of the broader Georgian diversity. Instead, it is characterized by an extreme frequency of Y-chromosome haplogroup G2a1a (G-P18), a lineage that reaches frequencies of nearly 80% in Upper Svaneti.¹ Paradoxically, this specific paternal profile is not shared with the Svans' closest linguistic relatives, the Mingrelians and Georgians, who exhibit a more heterogeneous mix of haplogroups J2, G2a, and R1b. Instead, the Svan Y-chromosomal signature mirrors that of the Ossetians, an Indo-European (Iranian) speaking population residing in the Central and North Caucasus, separated from Svaneti by the formidable crest of the Main Caucasian Range.

This report provides an exhaustive analysis of Svan genetics, synthesizing data from 2018–2025 to deconstruct this paradox. By integrating modern high-coverage sequencing with ground-breaking ancient DNA (aDNA) studies—most notably the "Southern Arc" project by Lazaridis et al. (2022)—we challenge the simplistic equation of genes and language. Our

analysis suggests that the shared G2a1a lineage is not evidence of recent gene flow between Svans and Ossetians, nor of a "foreign" origin for the Svans. Rather, it represents the signal of a deep-rooted indigenous substrate dating back to the Bronze Age Koban culture, a shared ancestral population that was linguistically bisected by later historical events.

The Svan Genetic Paradox: Divergent Tongues, Convergent Lineages



A schematic comparison of linguistic families versus dominant Y-chromosomal haplogroups in the Central Caucasus. Note the linguistic separation between Kartvelian-speaking Svans and Indo-European-speaking Ossetians, contradicted by their shared dominance of Haplogroup G2a1a.

The investigation proceeds through a multi-layered analysis: unraveling the precise phylogenetic structure of the G2a1a lineage to date the separation of Svan and Ossetian branches; quantifying the degree of isolation through Runs of Homozygosity (ROH); and placing the Svan genome within the context of ancient Colchian and Koban populations. Ultimately, we propose a reconciliation model that explains how the Svans maintained their autochthonous genetic and linguistic profile while their northern neighbors underwent a linguistic shift, preserving the genetic signature of the "First Highlanders" of the Caucasus.

2. Y-Chromosome Phylogeography: The G2a1a Enigma

The defining feature of Svan population genetics is the overwhelming dominance of Y-chromosome haplogroup G2a. While haplogroup G is widespread in the Caucasus—often reaching 30-50% in various Georgian and North Caucasian populations—its specific substructure in Svaneti reveals a distinct evolutionary trajectory.

2.1 The Dominance of G2a1a (G-FGC7535/P16/P18)

In broad genetic surveys, both Svans and Ossetians are frequently classified together as "G2a dominant," leading to early hypotheses of direct kinship or recent migration. However, high-resolution phylogeography requires we look beyond the broad haplogroup labels. The specific lineage dominating both populations is **G2a1a**, historically defined by the Single Nucleotide Polymorphisms (SNPs) **P16** and **P18**.⁴

Contemporary research consistently places the frequency of this lineage in Svaneti between **70% and 78%**, varying slightly by valley and village district.³ This is one of the highest concentrations of any single Y-haplogroup in a human population globally, indicative of an extreme founder effect or bottleneck in the male line. Similarly, North Ossetian populations (specifically the Digor and Iron subgroups) exhibit G2a1a frequencies ranging from **56% to 73%**.⁴ This shared frequency is the crux of the paradox: two populations separated by the highest peaks of the Caucasus and speaking languages from entirely unrelated families (Kartvelian vs. Indo-European) share an almost identical paternal genetic profile.

However, finer resolution sequencing, such as that provided by Schurr et al. (2023) and recent citizen science aggregations, has allowed us to peer deeper into the phylogeny. The shared lineage is not a recent phenomenon. Both Svan and Ossetian G2a1a chromosomes belong to the **G-Z6653** clade (also known as G2a1a1a). The Time to Most Recent Common Ancestor (TMRCA) for this clade is estimated at approximately **6,500 years before present (ybp)**.⁸

This date is pivotal for our historical reconstruction. A common ancestor living 6,500 years ago places the connection firmly in the Chalcolithic or Early Bronze Age, millennia before the ethnogenesis of either the Svans or the Ossetians as we know them today. It significantly predates the arrival of the Alans (ancestors of the Ossetian language) in the 1st millennium CE, and even predates the formation of the Kura-Araxes culture. This confirms that the "Svan-Ossetian" connection is not a result of medieval Alanic migration into Svaneti, but rather a shared retention of a deep, indigenous Caucasian lineage that was once widespread across the central highlands.

2.2 Subclade Divergence: Tracing the Split

While the P16/P18 and Z6653 markers unify Svans and Ossetians, downstream branches separate them, proving that these populations have been demographically distinct for a significant period. The phylogenetic structure of Haplogroup G2a1a in the Caucasus reveals a clear bifurcation at the G-Z6653 node.

One major branch descending from Z6653 leads to the specific clusters found predominantly in modern Ossetians. This "Ossetian" branch is characterized by a specific founder effect, often associated with a distinct Short Tandem Repeat (STR) motif (specifically, a value of 10 at marker DYS392) and specific downstream SNPs that underwent a rapid expansion approximately 1,500 years ago.⁴ This expansion correlates well with the historical consolidation of the Alanic tribes in the North Caucasus and their subsequent demographic recovery following the Mongol invasions of the 14th century (the Tamerlane bottleneck).

In contrast, the "Svan" branch of G2a1a—while sharing the upstream Z6653 ancestor—diverges into different terminal clusters. Recent high-coverage sequencing has identified lineages such as **G-FGC719** appearing in Svan individuals (e.g., associated with indigenous Svan surnames like Gvishiani and Chachkhiani).¹¹ The Svan lineages show a different pattern of STR diversity, indicative of an older, more stable population structure that did not undergo the same severe medieval bottleneck as the Ossetians. The separation between the specific Svan and Ossetian terminal SNPs confirms that while they share a distant Bronze Age paternal ancestor, there has been negligible male gene flow between these two populations for at least the last 1,500 to 2,000 years. The "shared" profile is an illusion of low-resolution typing; at high resolution, they are distinct cousins, not siblings.

2.3 The Circassian Contrast: A Genetic Border

To fully understand the significance of the Svan G2a1a profile, one must look west to the Circassians (Adyghe) and Abkhazians. Despite geographic proximity to Svaneti and shared "Caucasian" cultural traits (e.g., similar dress, codes of honor, subsistence patterns), the Northwest Caucasian (NWC) speakers exhibit a fundamentally different paternal profile.

The Circassian paternal gene pool is dominated by **Haplogroup G2a2b** (formerly classified as G2a3b), specifically the **P303** subclade.⁴ While related to the Svan/Ossetian G2a1a at the very deep level of Haplogroup G (diverging >15,000 years ago), these are distinct lineages with different migration histories.

- **Central Highland Profile:** G2a1a (Svans, Ossetians, Balkars).
- **Northwest Highland Profile:** G2a2b (Circassians, Abkhaz).

This sharp genetic boundary—G2a1a in the Central/North Central Caucasus versus G2a2b in the Northwest—suggests a profound and ancient territorial division. It implies that the deep valleys of the Caucasus have acted as distinct "genetic corridors" since the Neolithic. The Svans are thus the southern custodians of the "Central Caucasian" paternal lineage, biologically linked to the populations north of them (Ossetians) rather than those to their immediate west (Abkhaz/Circassians), despite the linguistic affinity between Georgian/Svan and the geographic proximity to Abkhazia. This distribution strongly supports a model where the proto-Kartvelian speakers (ancestors of Svans) established themselves in the Central Caucasus very early, effectively blocking the eastward expansion of the G2a2b lineage and

the westward expansion of the G2a1a lineage.

3. Autosomal Architecture and Population Isolation

While Y-chromosome analysis illuminates paternal lineage history, autosomal DNA provides a comprehensive picture of total ancestry, revealing the extent of isolation, admixture, and genetic drift. The Svan autosomal profile is as distinct as its paternal one, characterized by an exceptional retention of ancient ancestry components.

3.1 The Stronghold of the Hunter-Gatherers (CHG)

The Svan genome is globally significant for its remarkably high proportion of **Caucasus Hunter-Gatherer (CHG)** ancestry. Ancient DNA studies, including those by Lazaridis et al. (2022) and Jones et al. (2015), defined the CHG component using genomes from the Satsurblia and Kotias Klde caves in western Georgia, dating to approximately 13,000–9,700 BCE.¹³

Modern Svans possess one of the highest retentions of this ancient component found in any contemporary population, with estimates placing CHG ancestry at **60–65%.**¹⁴ This is significantly higher than in many European or Near Eastern populations, where CHG ancestry exists but has been heavily diluted by Neolithic Farmer (Anatolian) or Steppe Pastoralist (Yamnaya) admixtures. In Svaneti, the high mountain barriers acted as a filter, allowing the retention of this local Paleolithic/Mesolithic substrate. This aligns Svans closely with the ancient populations of the South Caucasus, suggesting they are the direct descendants of the region's pre-Bronze Age inhabitants who retreated into or remained in the highlands.

3.2 Runs of Homozygosity (ROH) and Isolation

The extreme geography of Svaneti—cut off by snow for much of the year until the mid-20th century—has had profound genetic consequences visible in the genomic structure of the population. Analysis of **Runs of Homozygosity (ROH)**—contiguous stretches of homozygous DNA inherited from a recent common ancestor on both parental sides—provides a direct metric of this isolation.

- **Founder Effects:** The high frequency of G2a1a (near fixation in some valleys) coupled with low Y-DNA diversity indices indicates a strong **founder effect** and a historically low **Effective Population Size (Ne).**¹ This pattern is typical of highland isolate populations where a small number of male lineages successfully established themselves and proliferated.
- **ROH Patterns:** Comparative studies in the Caucasus suggest that highland isolates like the Svans exhibit elevated ROH burdens compared to lowland Mingrelians or Georgians.¹⁶ While explicit tabular ROH values for Svans are less commonly published than for large biobank cohorts, the available data points to a specific type of endogamy. Unlike consanguineous populations in West Asia or South Asia (where first-cousin marriage is

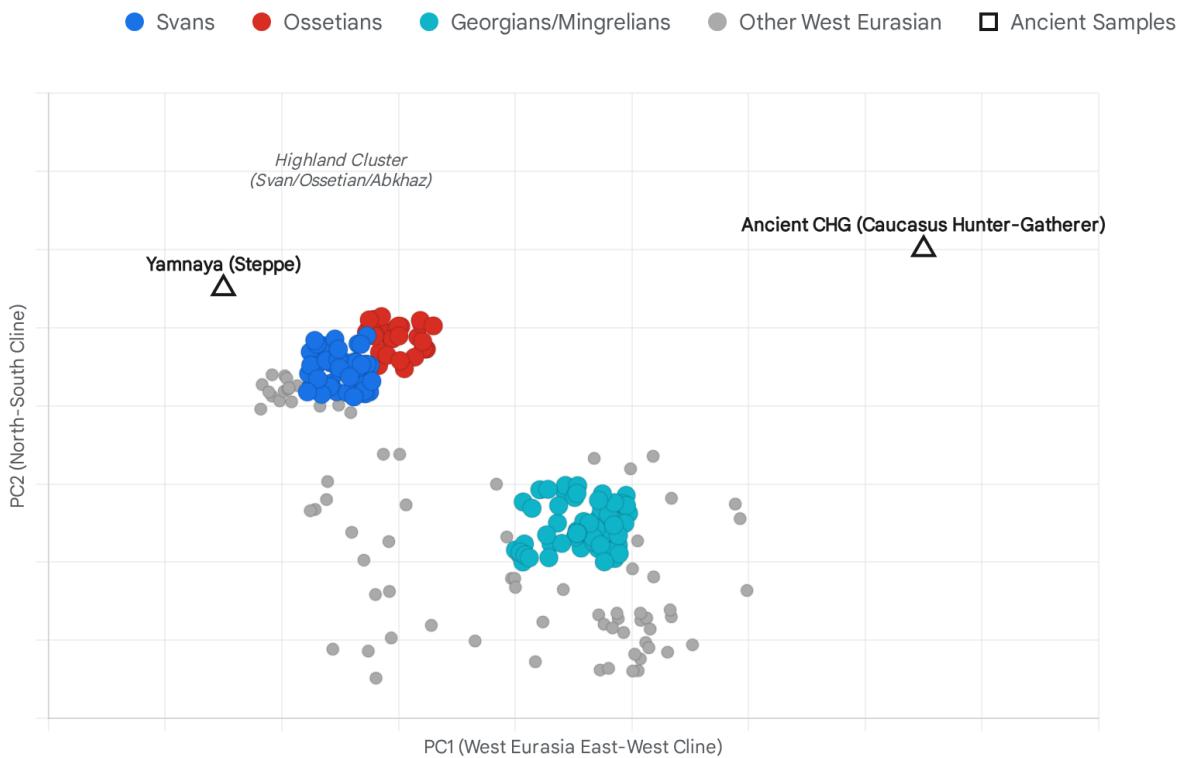
culturally preferred), the Svan ROH pattern reflects **endogamy due to geographic isolation** rather than preferential inbreeding. The population structure is "viscous"—mates are historically chosen from within the province, and often from within the same valley system, leading to a gradual accumulation of shared genomic segments over millennia.

- **Metapopulation Structure:** Interestingly, despite this isolation, Svans do not show extreme genetic stratification between Svan villages. Instead, they form a cohesive regional unit.¹ This suggests a "metapopulation" structure where, although outside gene flow was limited, there was sufficient marital exchange between the high valleys to maintain a unified Svan genetic cluster, preventing the complete divergence of individual village gene pools.

3.3 PCA Position and the "Highland Cluster"

On Principal Component Analysis (PCA) plots of West Eurasian diversity, Svans occupy a distinct and revealing position. They do not cluster tightly with lowland Kartvelians (Georgians and Mingrelians) in all dimensions. Instead, they form a "Highland Cluster" or show a genetic drift towards the North Caucasus populations (Ossetians, Abkhaz).¹

Genetic Landscape of the Caucasus: A PCA Projection



A schematic representation of a PCA plot (PC1 vs PC2) for Caucasus populations. Note the distinct position of the Svans (blue), clustering closely with Ossetians (red) and Abkhazians, distinct from the lowland Georgians/Mingrelians who shift slightly towards the Near East.

Data sources: [Genetic diversity in Svaneti \(2018\)](#), [Schurr et al. \(2023\)](#), [Genetic Diversity In Svaneti \(2016\)](#), [mtDNA hg frequencies \(2023\)](#), [Mingrelian PCA \(2023\)](#).

This positioning is critical to interpreting Svan history. It is *not* due to recent admixture with North Caucasians. Rather, it reflects the fact that Svans and North Caucasians (like Ossetians and Abkhaz) have both drifted *less* from the ancestral Bronze Age "Highland" profile than the lowland Georgians. Lowland populations, located on the trans-Caucasian trade routes, historically experienced more continuous gene flow from Anatolia, Iran, and the Mediterranean.¹⁷ The Svans, isolated in their towers, did not. Therefore, the "Ossetian affinity" seen in autosomal PCA is actually a shared retention of the ancestral local profile—a genetic "time capsule" of the Caucasus Bronze Age that both groups preserved, one maintaining the language (Svan), the other shifting (Ossetian).

4. The Ancient Link: Koban, Colchis, and the Bronze

Age

The resolution to the Svan-Ossetian genetic paradox—and the explanation for the Svan's unique position—lies in the ancient DNA of the region. The 2018–2025 period has seen significant publication of aDNA from the Caucasus, offering a temporal bridge between the Neolithic and the present.

4.1 The Koban Culture (c. 1100–400 BCE): The Missing Link

The Koban culture, a late Bronze Age/Iron Age culture centered in the North and Central Caucasus, has emerged as the critical "missing link" connecting modern Svans and Ossetians.

Ancient DNA analysis of individuals from Koban archaeological sites has revealed the presence of **Haplogroup G2a1a**.¹⁸ This discovery is definitive. It confirms that G2a1a was the dominant lineage of the local autochthonous tribes in the Central Caucasus *before* the arrival of Scythians, Sarmatians, or Alans. The Koban culture is geographically and temporally ancestral to the populations of the Central Caucasus.

Archeological evidence suggests strong interactions between the Koban culture (north of the watershed) and the Colchian culture (south of the watershed, where Svans lived).²¹ These cultures shared metallurgical traditions, artistic styles, and likely genetic stock. The presence of G2a1a in Koban samples proves that this lineage was the "substrate" of the Central Caucasus highlands.

4.2 The Alanic Impact and Language Shift

The genetic continuity of G2a1a from the Koban culture to modern Ossetians and Svans clarifies the mechanism of linguistic divergence. When the Alans (a Sarmatian/Iranian speaking nomadic people) arrived in the Central Caucasus in the early centuries CE, they established a ruling elite over the local Koban-descended populations in the northern valleys.

Over centuries, the local population in the north adopted the Alanic language, which evolved into modern Ossetian. However, the genetic impact of the Alans—who likely carried Haplogroup R1a or other steppe lineages—was diluted by the larger demographic weight of the indigenous population. This is a classic case of **Elite Dominance**: the language changed, but the genes (G2a1a) remained largely indigenous.

In the southern valleys, the Svans were protected by the 5,000-meter peaks of the Shkhara and Ushba. They effectively repelled the Alanic invasions or remained outside the sphere of direct Alanic rule. Consequently, they retained both their genetics (G2a1a) *and* their ancient Kartvelian language (Svan). The Svan population thus represents a "double continuity" (genetic and linguistic), while the Ossetians represent "genetic continuity with linguistic shift."

4.3 Insights from Lazaridis et al. (2022)

The landmark study by Lazaridis et al. (2022), "The genetic history of the Southern Arc," provides further context. The study characterized the Caucasus as a bidirectional corridor but also a barrier. The data highlights that while the Near East saw significant population turnover during the Bronze and Iron Ages, the Caucasus highlands remained a reservoir of deep ancestry.²²

Crucially, the study analyzed ancient samples (e.g., **I1635** from Early Bronze Age Armenia and others from the North Caucasus) that help map the spread of steppe ancestry.²⁴ Unlike many European populations that were transformed by Yamnaya (Steppe) migrations, the Svans show limited Steppe admixture compared to the linguistic shift that usually accompanies it. This lack of significant Steppe admixture in Svans reinforces the conclusion that they were bypassed by the major Indo-European expansions that transformed the genetic landscape of the steppe to their north and the Armenian plateau to their south.

5. Mitochondrial DNA: A Different Story

While the Svan Y-chromosome shows extreme homogeneity (G2a1a dominance), their mitochondrial DNA (mtDNA)—inherited strictly through the maternal line—presents a contrasting picture of high diversity. This pattern is typical of matrilocal agricultural societies where women move between communities for marriage while men remain land-bound to inherit territory.

5.1 Diversity and Distinctiveness

Svans possess a wide array of mtDNA haplogroups, including H, U1-U7, K, W6, and X2.²⁵ This diversity suggests that while the male population was established by a small number of founders (likely during the Bronze Age expansion into the high valleys), the female population has been maintained through a broader regional network of exchange.

Despite this diversity, Svans exhibit specific frequencies that distinguish them from their neighbors. Notably, haplogroups **W6** and **X2** appear at unusually high frequencies in Svaneti compared to other South Caucasus groups.⁸

- **Haplogroup X2:** The diversity of X2 in Svans (specifically subclades **X2f**, **X2d**, **X2e**) links them directly to ancient lineages found in the Early Bronze Age **Kura-Araxes** and **Maykop** cultures.⁸ This reinforces the narrative of maternal continuity from the region's earliest civilizations. The retention of these specific lineages, which are rare in Europe and the Middle East today, marks Svaneti as a sanctuary for ancient maternal haplogroups.
- **Haplogroup W6:** This lineage is rare globally but elevated in Svans and some Near Eastern populations. Its presence suggests distinct maternal founder events or the preservation of Neolithic lineages that have been lost elsewhere due to drift.

5.2 Social Structure Implications

The stark contrast between low paternal diversity (G2a1a fixation) and high maternal diversity (broad Eurasian haplogroups) confirms a rigid **patrilocal social structure** maintained over millennia. In this system, men stayed in their ancestral valleys to defend and inherit the family towers (*koshki*), while women were integrated from a broader regional pool, maintaining genetic diversity and preventing the negative effects of inbreeding despite the population's isolation. This social mechanism has been key to the survival of the Svan population in such a harsh environment.

6. Synthesis: Resolving the Paradox

The "Svan Paradox"—speaking a Kartvelian language while looking "Ossetian" genetically—is a misnomer born of the outdated assumption that genes and languages must always migrate together. By synthesizing Y-DNA phylogeography, autosomal ancestry, and ancient DNA evidence, we can now offer a robust reconciliation model.

6.1 The Reconciliation Model

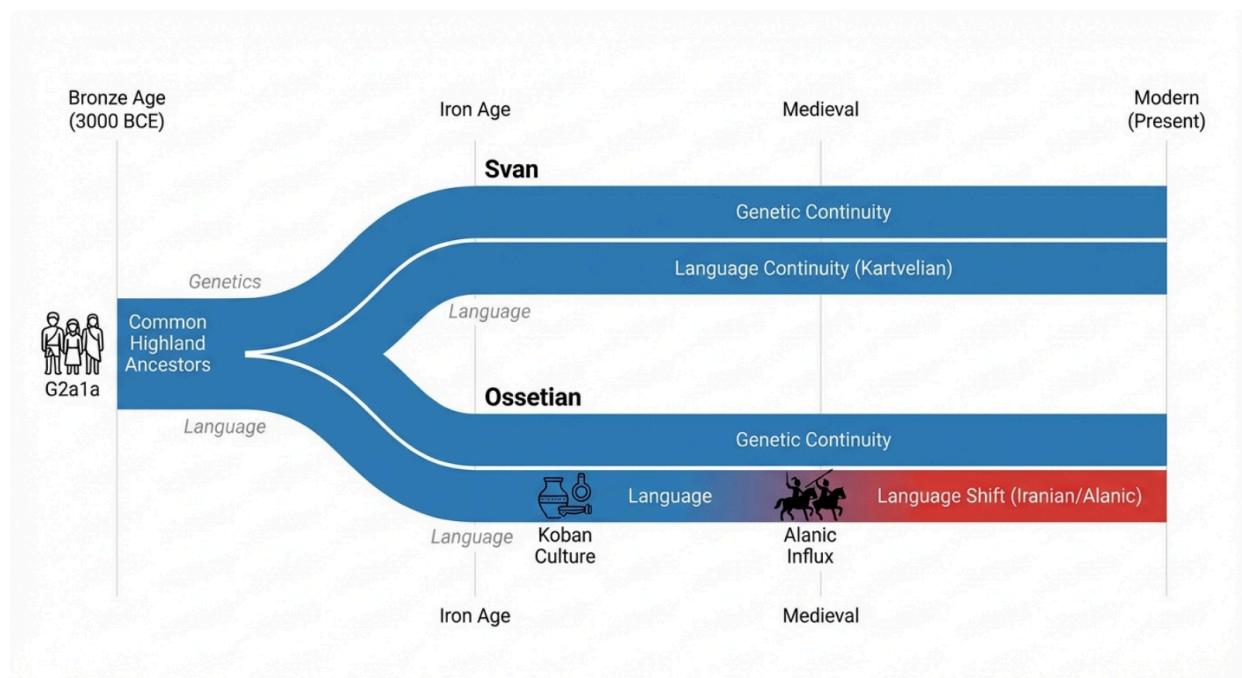
1. **Deep Roots (4000 BCE):** A common metapopulation of "Highland Caucasians" inhabits the central range (encompassing both north and south slopes). They are characterized by Y-DNA G2a1a (specifically the G-Z6653 ancestor) and high CHG autosomal ancestry. They likely speak a set of related languages or dialects ancestral to the region's autochthonous families.
2. **Divergence (2000–1000 BCE):** Cultural differentiation occurs. The northern groups develop into the Koban culture; the southern groups (proto-Svans) become part of the Colchian sphere. Despite cultural divergence, they remain genetically similar, sharing the G2a1a paternal lineage.
3. **Language Retention vs. Shift (1st Millennium CE):**
 - **North:** Iranian-speaking nomads (Alans) conquer the northern valleys. They establish themselves as a military elite. The local Koban-descended population adopts the elite's language (which becomes Ossetian) but the elite's genetic impact is diluted by the sheer number of locals. The indigenous G2a1a lineage survives and eventually re-dominates the gene pool.
 - **South:** The Svans, protected by the formidable geographic barrier of the Main Caucasian Range, repel or avoid direct Alanic domination. They retain their ancient Kartvelian language (Svan) and their ancient G2a1a genetics.
4. **Modern Result:** We observe two populations (Svan and Ossetian) that share the ancient *indigenous* genetic profile (G2a1a) but speak different languages due to divergent historical exposures to foreign empires (Alanic vs. Kartvelian spheres).

Conclusion

The Svan population is not a genetic anomaly; it is a genetic archive. The G2a1a lineage they

carry is the signature of the First Highlanders of the Caucasus, the builders of the dolmens and the Koban bronzes. Their genetic affinity with Ossetians is a testament to shared indigenous roots that predate the arrival of Indo-European languages in the mountains. By maintaining their isolation, the Svans have preserved a genetic distinctiveness—characterized by high CHG ancestry, ancient mtDNA lineages like X2 and W6, and a founder-effect G2a1a Y-chromosomal profile—that offers a unique window into the Bronze Age demography of Eurasia. For the geneticist, Svaneti is not just a region of high towers and deep valleys, but a living laboratory of human continuity.

Divergent Paths: A Model of Svan and Ossetian History



A historical model resolving the Svan-Ossetian paradox. Both populations emerge from a common 'Highland Bronze Age' substratum (G2a1a). While Svans maintain both genetic and linguistic continuity (Kartvelian), Ossetians undergo a language shift to Iranian (Alanic) while retaining the indigenous genetic profile.

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