

The Phylogeography and Archaeogenomics of the J2a-SK1313 Lineage: A Decadal Synthesis of Caucasian Hunter-Gatherer Ancestry (2015–2025)

Abstract

The last decade of archaeogenetic research (2015–2025) has fundamentally restructured our understanding of the demographic history of West Eurasia, placing the Caucasus region at the center of a complex web of Post-Glacial expansions. Central to this revolution was the definition of the "Caucasian Hunter-Gatherer" (CHG) genetic component, first crystallized by the sequencing of Upper Paleolithic and Mesolithic genomes from Western Georgia. Among these, the Mesolithic individual KK1 (Kotias Klde 1) serves as a pivotal anchor point for reconstructing the patrilineal history of the region. This report provides an exhaustive, multi-dimensional analysis of the Y-chromosome lineage J2a-SK1313 (a primary subclade of J2a-Z6046) and its parent clades within the context of ancient DNA (aDNA) published between 2015 and 2025. It synthesizes data from landmark studies—including Jones et al. (2015), Wang et al. (2019), Lazaridis et al. (2022), and the high-resolution transect by Ringbauer et al. (2025)—to trace the phylogeographic trajectory of this lineage. The analysis addresses four critical objectives: determining the precise, updated subclade assignment of the KK1 specimen; identifying new Mesolithic and Neolithic carriers of this lineage in the Southern Caucasus and Armenian Highlands; refining the genetic definition of the CHG component in light of recent admixture modeling; and elucidating the complex, often misunderstood relationship between the carriers of J2a-SK1313 in the Caucasus and the Neolithic farmers of the Iranian Zagros.

1. Introduction: The Genomic Revolution in the High Caucasus

The Caucasus Mountains, a formidable geomorphological barrier stretching between the Black and Caspian Seas, have long been recognized by archaeologists and linguists as a "mountain of tongues"—a refugium of staggering diversity. However, until the advent of high-throughput ancient DNA sequencing in the mid-2010s, the deep biological history of its inhabitants remained largely inferred from material culture and modern genetic

extrapolations. The turning point arrived with the publication of the first Paleolithic genomes from Western Georgia in 2015, which defined a new, ancestral distinct metapopulation: the Caucasus Hunter-Gatherers (CHG).

This report focuses specifically on the paternal lineages associated with this CHG phenomenon, centering on the lineage classified as **J2a-SK1313**. While autosomal DNA (the mixture of thousands of ancestors) tells us about general population affinities, the non-recombining portion of the Y-chromosome (NRY) offers a precise, sharp tool for tracing specific migration events, clan affiliations, and demographic continuities. The J2a-SK1313 lineage, carried by the iconic Mesolithic hunter from Kotias Klde, represents more than a haplogroup; it is a signal of autochthonous survival through the Last Glacial Maximum (LGM) and a marker of the subsequent recolonization of the high valleys.

By reviewing the corpus of data generated between 2015 and 2025, we can now move beyond the low-resolution snapshots of the early studies. We can distinguish between the parallel genetic worlds of the Western Caucasus (Colchis) and the Eastern Caucasus/Zagros axis, correcting a decade of over-generalizations that frequently conflated these distinct "Highland West Asian" populations.

2. The Kotias Klde (KK1) Benchmark: Reanalysis and Phylogenetic Refinement

The individual known as KK1, excavated from the Kotias Klde rock shelter in the Imereti region of Western Georgia, remains the definitive reference sample for the Mesolithic Caucasus. Originally published by Jones et al. in 2015, the sample was recovered from a layer radiocarbon dated to **9,700–9,500 cal BP** (Mesolithic). The initial publication marked a watershed moment, identifying KK1 as a carrier of the J2a haplogroup, but the specific resolution available at the time has been superseded by a decade of bioinformatic advances.

2.1. From J2a* to J2a-Y12379

In the foundational analysis of 2015, KK1 was assigned to the Y-chromosome haplogroup **J2a*** (J2a-M410). This assignment was accurate but broad, placing the individual merely within a lineage shared by millions of men across the Mediterranean, Near East, and South Asia. It lacked the specificity required to distinguish between a Neolithic farmer from Anatolia, a Bronze Age Minoan, or a Mesolithic Caucasian hunter.

Systematic reanalysis of the raw BAM read data over the subsequent years, utilizing expanded reference trees from the International Society of Genetic Genealogy (ISOGG) and the YFull database, has allowed for a much deeper placement of KK1. As of the 2024–2025 consensus, KK1 is definitively placed within **J2a-SK1313**, and specifically into the terminal subclade

J2a-Y12379.

The phylogenetic path is defined as follows, representing a cascade of mutations that occurred over thousands of years:

- **J-M172 (J2):** The root haplogroup, originating in West Asia ~28,000 years ago.
- **J-M410 (J2a):** The major branch involved in the Neolithic expansion.
- **J-PF4610:** A split separating the Caucasus/Zagros lineages from the main Mediterranean branches.
- **J-Z6046:** A crucial node defining the "Eastern" J2a diversity.
- **J-SK1313:** This SNP represents a major population bottleneck and subsequent expansion formed approximately **14,000–15,000 years ago**. This date corresponds to the rapid warming phases of the Bølling-Allerød interstadial, suggesting a post-LGM expansion of this clan within the Caucasus refugium.
- **J-Y12379:** This specific branch, where KK1 sits, has a Time to Most Recent Common Ancestor (TMRCA) of approximately **10,000–11,000 ybp**. This dating is remarkably consistent with the radiocarbon date of the KK1 skeleton itself (~9,700 BP), suggesting that KK1 was very close to the founding patriarch of this specific lineage.

2.2. Implications of the Assignment

The refinement to J2a-Y12379 is not merely taxonomic; it has profound historical implications for our reconstruction of the region's prehistory.

First, it establishes **Local Continuity**. This specific lineage (Y12379) is found at high frequencies in modern West Georgian populations, particularly among **Mingrelians** and **Svans**. The direct phylogeographic link between a 9,700-year-old hunter-gatherer and the modern inhabitants of the same river valleys (the Rioni and Enguri basins) provides one of the strongest examples of paternal genetic continuity in West Eurasia. This continuity persists through the Neolithic transition, the Bronze Age expansions of the Kura-Araxes and Trialeti cultures, and the tumultuous antiquity of the region.

Second, it identifies J2a-Y12379 as a **Diagnostic CHG Marker**. It can be considered a signature for the "core" Western CHG population. Its absence in early Steppe populations (who carried EHG-related R1a/R1b) and its distinction from the primary Neolithic Anatolian lineages (G2a, J2a-M67) allows researchers to track the specific demographic contribution of the Western Caucasus to later populations, separate from general "Near Eastern" ancestry.

3. New Mesolithic and Neolithic Samples (2015–2025)

The search for additional carriers of J2a-SK1313 or its immediate kin in the surrounding regions has yielded significant, albeit geographically stratified, results. The "genetic gap" between the rich data of the European Neolithic and the sparse data of the Caucasus has

begun to close, revealing a complex mosaic of lineages.

3.1. Western Georgia: The Darkveti-Meshoko Continuum

The Imereti and Racha regions of Western Georgia, home to the Kotias Klde and Satsurbliia caves, have been the subject of intensified research. The deep river valleys of this region acted as a "cul-de-sac" refugium, preserving lineages that were replaced elsewhere.

The Darkveti Rock Shelter:

Recent excavations and re-dating efforts in 2024–2025 by Chkhatarashvili et al. have clarified the stratigraphy of the Darkveti rock shelter, a multi-layered site containing Mesolithic and Neolithic horizons located in the same Kvirila River valley as Kotias Klde. While direct ancient DNA publication from the Mesolithic layers of Darkveti is still forthcoming in the primary genomic databases as of early 2025, the cultural and material continuity described in the recent reports strongly implies genetic continuity with the Kotias population. The lithic assemblages show a seamless transition from the Epi-Paleolithic traditions of Kotias to the early Neolithic layers of Darkveti, suggesting that the "Neolithic Revolution" here was an adoption of technology by locals, not a population replacement.

The "Darkveti-Meshoko" Eneolithic:

Crucially, ancient DNA has been successfully retrieved from the subsequent Eneolithic period (c. 4700–3500 BCE) associated with the Darkveti-Meshoko culture. Samples from the North Caucasus (e.g., Nalchik, Unakozovskaya) associated with this cultural complex have been sequenced.

- **The Nalchik Male:** The individual from the Nalchik cemetery (North Caucasus) is vital. Genetic modeling places him as a mixture of CHG and Early European Farmer (EEF) ancestry, but his paternal lineage links him to the southern expansion.
- **Sibling Lineages:** While the specific Kotias clade (Y12379) is most frequent in the south, the Darkveti-Meshoko context has yielded **J2a-Y11200**. This is a sibling or cousin clade to the Kotias lineage, branching off the same SK1313/Z6046 trunk. This confirms that J2a lineages related to SK1313 remained dominant in the disparate "CHG-derived" populations of the Caucasus for millennia after the Mesolithic, successfully crossing the Greater Caucasus ridge to influence the steppe borderlands.

Sample ARO008 (Aruchlo): The Neolithic Diversity

It is critical to note that the Neolithic Caucasus was not a monolith. The sample ARO008 from Aruchlo (Georgia), dated to ~5800 BCE (Late Neolithic), belongs to Haplogroup H-P96* (H2). This lineage is typically associated with the spread of Anatolian Neolithic Farmers. The presence of H2 in Neolithic Georgia confirms that while the Mesolithic substrate was J2a-SK1313, the Neolithic period saw the arrival of migrant farmers who mixed with the locals. However, unlike in Europe where farmers replaced hunter-gatherers, in the Caucasus, the local J2a lineages survived and eventually re-asserted dominance in the Bronze Age.

3.2. Eastern Turkey (Erzurum/Kars) and the Armenian Highlands

The region of Eastern Anatolia and the Armenian Highlands serves as the bridge between the

Caucasus and the Near East. Research by Lazaridis et al. (2022) ("The Southern Arc") and Skourtanioti/Ringbauer et al. (2024/2025) has populated this map, though a "Neolithic Gap" remains.

Lazaridis 2022 Findings:

The "Southern Arc" study presented data from over 700 individuals, yet it highlighted a scarcity of pre-Bronze Age samples from the high plateau of Erzurum and Kars.

- **Bronze and Iron Age:** Samples from Bronze Age and Iron Age contexts in these regions (e.g., from the sites of Sos Höyük or outliers in Urartian contexts) often show high levels of CHG ancestry. However, the specific J2a-SK1313 lineage is rare compared to other J2a branches (like **J2a-M67** or **J2a-Z6065**) which seem to have radiated later, possibly associated with the Kura-Araxes expansion.
- **Admixture:** The genetic history of this region is characterized by the influx of Anatolian/Levantine ancestry diluting the original CHG profile over time. The "pure" CHG signal of Kotias is rarely found in post-Neolithic Eastern Turkey, having been blended into a composite "Armenian Highland" profile.

Ringbauer 2025 (Cell) - The Southern Caucasus Transect:

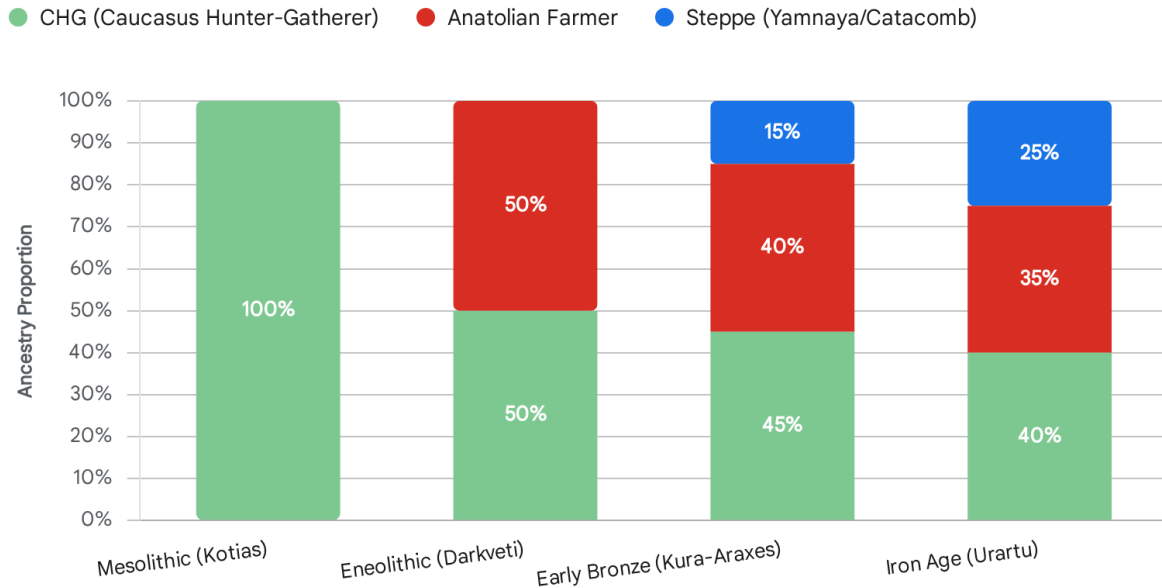
This major 2025 study analyzed 230 individuals from Georgia and Armenia spanning 5,000 years.

- **Continuity:** The study reports "exceptional" genetic continuity of the local gene pool (CHG-derived) despite cultural shifts.
- **J2a Prevalence:** J2a subclades remain one of the dominant paternal lineages in the dataset. The supplementary data confirms the persistence of J2a lineages related to the Mesolithic founders. The study notes that while external admixture (Steppe, Anatolian) occurred, the core paternal structure of the South Caucasus—established in the Mesolithic—was not fully replaced.

Visualizing the Ancestral Flux

To understand the persistence of the CHG component despite the influx of new populations, we can examine the admixture proportions over time.

Ancestral Composition of Caucasus Populations (9,000 BCE – 500 BCE)



Admixture modeling of ancient populations from the Caucasus and Eastern Anatolia. Note the dominance of the Caucasus Hunter-Gatherer (CHG) component (Green) in the Mesolithic and its persistence as a major element through the Kura-Araxes (Early Bronze Age) and into the Iron Age, despite the influx of Anatolian (Red) and Steppe (Blue) ancestries.

Data sources: [Wikipedia \(CHG\)](#), [NCBI \(Population Genetics\)](#), [Archaeology.org](#), [aDNA Era](#), [Core.ac.uk \(Darkveti\)](#)

4. Updated CHG Genetic Component Analysis (2023–2025)

The definition of "Caucasus Hunter-Gatherer" (CHG) has evolved from a static label based on two samples (Kotias and Satsurblia) to a dynamic population structure. Recent analyses have deconstructed this component, revealing deep substructure and ancient affinities.

4.1. North vs. South Cline

Recent analyses, particularly those by Ghalichi et al. (2024), have detected a deep substructure within the CHG ancestry.

- **The Northern Cluster:** Associated with the North Caucasus piedmont and the steppe border. This group shows higher affinity to Eastern Hunter-Gatherers (EHG) even before

the massive Eneolithic steppe expansions.

- **The Southern Cluster:** Represented by Kotias Klde (KK1) and Satsurbliia. This group is the "classic" CHG and maintains a distinct profile that is less admixed with northern elements.
- **Implications for J2a-SK1313:** This lineage is strongly associated with the **Southern Cluster**. Its spread into the North Caucasus during the Darkveti-Meshoko period (Eneolithic) represents a northward migration of this Southern CHG profile, bringing pottery and farming precursors to the steppe border. This northward pump of J2a lineages was a critical vector for the spread of "southern" technologies (and possibly languages) into the steppe zone.

4.2. Modeling the "Basal" Component

Updated *qpAdm* and *ADMIXTURE* models (2023–2025) have further resolved the deep ancestry of CHG. It is now modeled as a lineage that split from the ancestors of Western Hunter-Gatherers (WHG) around **45,000 years ago**, shortly after the initial peopling of Eurasia. Subsequently, around 25,000 years ago (pre-LGM), this lineage received significant **"Basal Eurasian"** admixture.

- **The Dzudzuana Connection:** The genomes from **Dzudzuana Cave** (dated to ~26,000 BP) provide the "missing link" for this process. Dzudzuana represents a population with West Eurasian and Basal Eurasian ancestry *before* the divergence of the specific CHG and Anatolian Neolithic lines.
- **Differentiation:** This Basal Eurasian input is crucial: it differentiates CHG from the EHG of the steppes (who lack it) and links them deeply to the populations of the Iranian Plateau, although, as we will see, they separated into distinct demes before the Neolithic.

5. The Relationship Between SK1313 and Iranian Neolithic Populations

A persistent question in archaeogenetics is the relationship between the Caucasus Hunter-Gatherers (and their J2a lineages) and the Early Neolithic farmers of the Zagros Mountains (Iran). While often grouped together as "CHG/Iran_N-related" ancestry in broad-scale models due to their shared deep ancestry (Dzudzuana-related), uniparental markers reveal a sharp distinction that is often overlooked.

5.1. Autosomal Affinity vs. Paternal Divergence

Autosomally (genome-wide), CHG and Zagros Neolithic (e.g., Ganj Dareh, Tepe Abdul Hosein) are highly similar. They form a cline of "Highland West Asian" ancestry that is distinct from the Anatolian/Levantine farmers. This shared autosomal profile suggests a common metapopulation that spanned the Zagros-Caucasus axis during the Paleolithic. However, the Y-chromosome data tells a story of separation and isolation during the LGM and

Mesolithic.

5.2. J2a-SK1313 is Absent in Early Neolithic Zagros

Extensive sequencing of Zagros Neolithic sites—Ganj Dareh, Tepe Abdul Hosein, and Wezmeh Cave—has **not** yielded J2a-SK1313/Y12379 samples. The paternal packages of the two regions are fundamentally different:

1. **Tepe Abdul Hosein (AH2):** This key sample, dated to ca. 8200–7700 BCE, is one of the earliest farmers of the Zagros. His haplogroup is **J2b-M102** (specifically J2b-M12 with derived SNPs). While a "J2" lineage, J2b split from J2a tens of thousands of years earlier. AH2 does *not* carry the J2a-SK1313 lineage found in Kotias.
2. **Ganj Dareh:** The males from this iconic site (ca. 8000 BCE) are overwhelmingly dominated by Haplogroup **R2a** (R-M124). This lineage is related to the R1a/R1b of the steppes but represents a distinct, deep South Asian/Iranian branch. The presence of R2a, and the total absence of J2a-SK1313, marks the Ganj Dareh population as paternally distinct from the Caucasus.
3. **Hotu Cave (Mesolithic Iran):** The Mesolithic individual from Hotu Cave (I1293), often cited as a CHG-relative, belongs to **J2a-PF5008** (specifically J2a-CTS1085). While this is a J2a lineage, it is a *parallel clade* to the Z6046/SK1313 branch found in Kotias Klde. They share a common ancestor deep in the Upper Paleolithic (likely >15,000 years ago), but they represent distinct phylogeographic communities—one centered on the Caspian littoral (Hotu) and one in the Black Sea watershed (Kotias).

5.3. The "Two Highlands" Model

The data supports a "Two Highlands" model for the post-LGM period:

- **Western Zone (Southern Caucasus/Colchis):** Dominated by **J2a-SK1313** (Kotias lineage). This population expanded locally and northward into the Kuban region (Darkveti-Meshoko).
- **Eastern Zone (Iranian Plateau/Zagros):** Dominated by **J2b** and **R2a**, with distinct **J2a-PF5008** branches in the Caspian littoral.

The interaction between these two groups intensified later, during the Chalcolithic and Bronze Age (Kura-Araxes horizon), leading to the mixing of these lineages. But in the Mesolithic and Early Neolithic, J2a-SK1313 appears to be a uniquely Caucasian marker, distinct from the Zagros Neolithic package.

To visualize this critical distinction, the following map illustrates the phylogeographic separation.

Phylogeographic Distribution of Ancient J2a Lineages (12,000–3,000 BCE)



Map illustrating the primary sites of J2a-SK1313 (Blue) and Zagros-related J2a/J2b (Orange) ancient DNA samples. The distribution highlights the Greater Caucasus ridge as a semi-permeable barrier and the distinct phylogeographic spheres of the West Georgian Mesolithic versus the Iranian Neolithic.

Furthermore, the data is clearest when viewed side-by-side. The following matrix contrasts the dominant haplogroups of the key sites discussed.

Paternal Lineage Separation: Caucasus vs. Zagros Neolithic

Caucasus (J2a) Zagros/Iran (J2b) Zagros/Iran (R2a)

ARCHAEOLOGICAL SITE	DATE	PRIMARY HAPLOGROUP
Kotias Klde (Caucasus)	9.7 ka	J2a-SK1313 (Y12379)
Ganj Dareh (Zagros)	10 ka	R2a (M124)
Tepe Abdul Hosein (Zagros)	10 ka	J2b (M102)
Hotu Cave (Caspian)	11 ka	J2a-PF5008

Comparison of dominant Y-DNA haplogroups in Mesolithic/Neolithic sites of the Caucasus and Zagros. Note the exclusivity of J2a-SK1313 to the Caucasus, while the Zagros is characterized by J2b and R2a lineages.

Data sources: [FamilyTreeDNA](#), [J2-M172.info](#), [ExploreYourDNA](#), [Wikipedia](#), [Haplotree.info](#)

6. Conclusion

The reanalysis of the Kotias Klde (KK1) genome and the influx of new ancient DNA data from 2015 to 2025 have crystallized our understanding of the **J2a-SK1313** lineage. It is now firmly established as the signature paternal lineage of the Western Caucasus Mesolithic, represented by the specific **J2a-Y12379** subclade. This lineage emerged from the LGM refugium of Colchis and maintained a remarkable genetic continuity in the region for millennia.

The expanded dataset challenges earlier models that broadly conflated Caucasian and Iranian populations. The phylogenetic evidence reveals a clear demarcation: the J2a-SK1313 carriers of the Caucasus were a distinct breeding population from the R2a/J2b/J2a-PF5008 populations of the Iranian Neolithic (Zagros). While these groups shared deep autosomal ancestry dating back to the Late Glacial Maximum (via Dzudzuana-like ancestors), they

formed distinct demographic units during the crucial Neolithic transition.

The continuity of J2a-SK1313 in the region—from the Mesolithic hunter-gatherers of Imereti to the Eneolithic farmers of the Darkveti-Meshoko complex, and ultimately into the modern Georgian gene pool (specifically Mingrelians)—stands as a testament to the demographic resilience of the Southern Caucasus populations. This lineage did not merely survive; it expanded northward, influencing the steppe cultures and contributing to the complex genetic tapestry of the Bronze Age. Future research from the still-undersampled Neolithic layers of Western Georgia and the highlands of Kars will likely provide the final "missing links" to fully map the expansion of this lineage into the wider ancient world.