PHYLOGENETIC ANALYSIS OF Y-CHROMOSOME LINEAGES IN POPULATIONS FROM SVANETI AND MINGRELIA/SAMEGRELO (WEST GEORGIA)

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ABSTRACT

Introduction. Given the ethno-cultural diversity of the Caucasus, the issue of the ethnogenesis of the populations living there remains an outstanding scientific problem. To investigate this issue, DNA sampleswere collected during scientific expeditions conducted in North-West Georgia (Svaneti and Samegrelo) between 2012-2017. They were analyzed for Y-chromosome diversity from a population genetic perspective and the results were published. A subject of interest remains the phylogenetic history of the paternal haplogroups identified there. The present work is an attempt to elucidate this history using these Y-chromosome data.

Materials and Methods.Y-chromosome STR data for 93 men living in Svaneti (northwestern mountainous region of Georgia, total population of about 12,000) and 364 men living in Samegrelo (northwestern region of Georgia, total population of about 500,000) were analyzed. The"Kilin-Klyosov calculator" software was used for the phylogenetic and coalescence analysis of these data.

Results and Conclusions. It was determined that the Svaneti population, in which there is a high concentration of G2a1 (up to 80%), probably separated from the Proto-Georgian founding population in the Late Bronze Ageand split from theancestor of the Samegrelo population around 3,680 ± 420years before present. This interpretation issupported by archaeological studies, which describe the oldest stationary settlement in Upper Svaneti precisely in the Late Bronze Age. The results obtained are further consistent with the generally accepted linguistic hypothesis for the emergence of Kartvelian languages.

Key words: DNA, trees, lineages, language, history, haplogroup, haplotype, short tandem repeat (STR)

აბსტრაქტი.

შესავალი. გამომდინარე კავკასიის ეთნოკულტურული მრავალფეროვნებიდან, აქ მცხოვრები პოპულაციების ეთნოგენეზის საკითხი ერთ-ერთ გამორჩეულ სამეცნიერო პრობლემად რჩება. 2012-2017 წლებში ჩრდილო-დასავლეთ საქართველოში (სვანეთი და სამეგრელო) ჩატარებული სამეცნიერო ექსპედიციის დროს შეგროვებული გენეტიკური მასალა შესწავლილი იქნა პოპულაციური გენეტიკური თვალსაზრისით და შედეგები

გამოქვეყნებული იქნა. ინტერესის საგნად რჩებოდა მასალის ფილოგენეტიკური ანალიზი. წინამდებარე ნაშრომი ამ კითხვებზე პასუხის გაცემის მცდელობაა.

მასალები და მეთოდები. გაანალიზდა სვანეთში (საქართველოს ჩრდილო-დასავლეთ მთიანი რეგიონი, დაახლოებით 12,000 მოსახლე) მცხოვრები 93 მამაკაცისა და სამეგრელოში (საქართველოს ჩრდილო-დასავლეთი რეგიონი, დაახლოებით 500,000 მოსახლე) მცხოვრები 364 მამაკაცის Y-ქრომოსომის STR მონაცემები. ამ მონაცემების ფილოგენეტიკური და შერწყმის ანალიზისთვის გამოყენებული იქნა „კილინ-კლიოსოვის კალკულატორის“ პროგრამა.

შედეგები და დასკვნები. დადგინდა, რომ სვანეთის მოსახლეობა, რომელშიც G2a1-ის მაღალი კონცენტრაციაა (80%-მდე), სავარაუდოდ, გვიან ბრინჯაოს ხანაში გამოეყო პროტოქართული დამფუძნებელი მოსახლეობიდან და გამოეყო სამეგრელოს მოსახლეობის წინაპარს დაახლოებით 3,680 ± 420 წლით ადრე. ეს ინტერპრეტაცია დასტურდება არქეოლოგიური კვლევებით, რომლებიც აღწერენ ზემო სვანეთის უძველეს სტაციონარულ დასახლებას ზუსტად გვიან ბრინჯაოს ხანაში. მიღებული შედეგები ასევე შეესაბამება ქართველური ენების წარმოშობის ზოგადად მიღებულ ლინგვისტურ ჰიპოთეზას.

საკვანძო სიტყვები: დნმ, ხეები, შტოები, ენა, ისტორია, ჰაპლოჯგუფი, ჰაპლოტიპი, მოკლე ტანდემური გამეორება (STR)

INTRODUCTION

Thanks to its ethnic composition and linguistic diversity, Caucasus is one of the most interesting regions in the world. While many languages (about 70) have been recorded and studied, only Georgian and Armenian have their own scripts, which are rather old and rich from the point of view of source studies.

Another language emerging in the Caucasus has been preserved in the form of separate fragments of epigraphs and manuscript and in spoken form by the Udi (Uti), a small ethnic group living in the region. From a linguistic point of view, most Georgian scientists (Iv. Javakhishvili, I. Abuladze, A. Shanidze, A. Chikobava, C. Panjavidze, E. Jeiranashvili, Z. Aleksidze, et al.) consider the Udi language (together with cognate languages) as being CaucasianAlbanian (Sharabidze: 2003, 190-191). Over time, the Udi created an Albanian state and culture,with ancient authors mentioning more than two dozen tribes (Gardamanians, Gargarians and Tsavdians) and kings inhabiting this area (Topchishvili: 2007,160).

This ethno-cultural diversity of the Caucasus has been shaped by many factors. Among them are features of the landscape, which is dominated by high mountains. These highlands likely induced conservation of linguistic and ethnographic features but also stimulated linguistic alienation of the populations of the same origin, resulting in the emergence of dialects and languages.

In addition to this topographic influence, other historical events have contributed the cultural diversity of populations from the region. Ethno-cultural populations from the southern steppes of Russia and regions of Central Asia exerted anorthern influence, while physical and cultural contacts with the Middle East were responsible for southern influences (Vashakidze: 2023. 65-66).

Studies of the ancient political, social and economic history of the Caucasus are based upon the data given in Hittite, Assyrian Urartian, Greco-Roman, Persian, and later Georgian, Armenian and Arabic written sources. In the context of these documents, these sources (Caucasus Antiquus. 2022.) and Greek textsindicatethat tribes of Kartvelian origin (great union of Diaukhi/ Diaokhi, Colchis, Mushkis)had a clan based social organization by at leastthe middle of the Late Bronze Age and formed states by the end of the same epoch. The situation did not change almost until the end of the ancient period followed in Caucasus by feudalism and the appearance of multiple state structures (Caucasus Antiquus, 2022).

In the Caucasus, religion played asignificant role in shaping culture diversity there. A major influence came from confession/dogmatic forms of Christianity (e.g., Georgian and Armenian Christianity) between 300-500 CE. The influx of other cultural elements also came from strong external impacts such asinvasions, absorptioninto large empires (e.g., Russia), and the spread of other religions (e.g., Islam and Judaism) in the North Caucasus and South-East Black Sea Region.

Only in Georgia, three distinct languages are spoken, including Georgian, Megrelian-Laz (i.e., "Zan languages") and Svan.They are grouped into the Kartvelian language family. In addition, there are about 20 different regions in Georgia, all of them having special ethnographic characteristics, where the Georgian language is spoken as different dialects (Vogt H:1938, 1961; Chikobava A: 1965; Boeder W: 2005.). The whole population developed a strong self-identity signified by the word "Kartveli" (Georgian) during the 20th century. Today, the majority of Laz-speaking populations live within the borders of present-day Turkey.These people have close ethno-cultural and historic connections with the common Caucasian world.

Historical and Linguistic Data

For centuries, there have been debates about the possible ethno-genesis of Caucasian peoples and the origin of Caucasian languages. Likewise, scholars have discussed various ideas about the history of the Kartvelian language family.

Today, the territory between the right banks of Rioni and Tskhenistskhali Rivers to Ghalidzga, and even further, is settled by Mingrelian-speaking people. From historic and ethnographic perspectives, Mingrelia adjoins northeastern Svaneti. To the southeast, it is bordered by Imereti. In the historical and toponymic context, populations speaking this language spread to the Likhi range and, in a later period, into the territory of ShidaKartli.

Shida Kartli has been populated by Kartvelian speakers since ancient times. Some local toponyms have Georgian-Zan and Svan or Georgian-Zan parallel forms. Movements from the highlands to the lowlands over manycenturiesleft a certain imprint on the composition of the population (Gvasalia J: 1983. 164). Even from the point of view of archaeology, the population of west Georgia and ShidaKartli have had close cultural and ethnic connections since at least the Late Bronze Age (Kuftin: 1949. 46, 63, 86; Gagoshidze:1964. 36.). From the late 7th century BCE, during the reign of Sarduri II, the Kingdom of Colchis included west Georgia as well as a part of east Georgia (Gamkrelidze: 2021. 4).

Archaeological evidence points to cultural affinities between Shida Kartli and west Georgia since the Eneolithic era. Accordingly, the political entity on the territory of west Georgia is the state known as Colchis. It seems that populations migrated from West Asia to the South Caucasus, which can be traced in changes in material culture (Japaridze: 1976. 252-314; Japaridze: 2006, 271). Deity names from Asia Minor were probably brought with this expansion, such as Armazi and Zaden, who had already been worshiped in Georgia in the early ancient era (Gagoshidze: 1964. 86, 87).

The viewpoints about the settlement of peoples who spoke Kartvelian languages may be divided into two models, (a) a single origin and (b) multiple, diverse origins.The first model postulates that Kartvelian languages originated within a single ethnic group speaking a proto-Kartvelian language that differentiated at different historical stages. People who spoke these languages lived in the Caucasus and eastern Anatolia, with their sub-ethnic and cultural features becoming differentiated due to internal and external factors. The language which differentiated (dialects turned into languages) into several languages is called proto-Kartvelian language. Derivation of different Kartvelian languages from this proto-language was preconditioned by the weakening of language contacts between regions, which could be caused by external factors such as relative territorial remoteness and arduous natural barriers (a mountain, a river, etc.) (Chikobava: 1948. II, 8). The second model presupposes the autochthony of the populations who spoke Kartvelian languages (Janashia: 1952, II).

According to one classification of Kartvelian languages, the Mingrelian-Chan language (s.c.Zan), together with Svan and Georgian itself, belongs to the Kartvelian (South Caucasian) group of the so-called Caucasian or Iberian-Caucasian family of languages. The term "Iberian-Caucasian languages" implies some genealogical features of these languages, similar to Indo-European, Semitic and other language families (Bopp: 1847; Muller: 1855; Marr: 1926б.3-4). Since the beginning of the 20th century, there have been discussions about the existence of certain parallels between the Kartvelian languages and the Sumerian (Fänrich: 1981. 89), Khathite (Girbal: 1986. 160-161), Hittite (Hrozny: 1938. 31), Hurrian (Diakonov. M: 1958. 26 and fol.; Wilhelm: 1985.), and Urartian (Melikishvili: 1954, 47-49) languages.

However, Caucasian languages also contain a geographic context (Chikobava: 1965. 4). Linguistically, the Svan language was preceded by the Zan language because sibilant variants could be deposited only after the formation of Zan language as an independent unit. As for Abkhasian-Adighe linguistic elements, they were internalized in the Svan language that had been greatly influenced by Zan (Chikobava: 1948. 261, 264).

According to G. Klimov, theseparationof Svan fromthe common Kartvelianlanguagebegan in the19th century BCE, while Zan-Georgian divergence began in the 8th century BCE (Klimov: 1959). This scenario is also supported by T. Gamkrelidze and G. Machavariani (Gamkrelidze, Machavariani: 1965).The era of Georgian-Zan unity almost completely comprises the Late Bronze Age (Mamulia: 1976. 128).

It goes without saying that the dates established by means of glottochronology and those obtained either from archaeological/historic sources or through studies carried out by means of modern advanced technologies have varied. Bayesian analysis of these languages supports an older dating (7th millennium BCE) of the ancestral Kartvelian language differentiation (Gavashelishvili, et al: 2023). It is worth mentioning that the findings fromthese studiesare reliant on the contents of the database created and uploaded for analysis by the respective authors.

In the scientific literature, various opinions on the initial emergence of the Svan population have been expressed (Marr: 1913. 32, 34; Janashia: 1959. III, 300; Melikishvili: 1965. 65; Mikeladze: 1974. 10-12; Mibchuani: 1989. 11,12; Boeder: 2005). According to one model, Svan and Zan (Mingrelian-Laz-Chan) languages shifted in the form of a common proto-Kartvelian ethnic stream from the south to the north (Javakhishvili: 1951. 428-429; Lehmann-Haupt: ,1937, 262.).A contrasting model proposes that, instead of migrating during the Hittite-Assyrian and Urartian period, Kartvelian tribes lived within vaster territories and their political centers constantly shifted to the north. In accordance with this latter hypothesis, Svans reached the territory of present-day Georgia first during the late 2nd millennium BCE. They were followed by Mingrelians and then Kartvelis or Kartis (Janashia: 1988a: 373). As a consequence, finally was established the Iberian kingdom with the capital in Armazi-Mtskheta (Janashia:1988b, 346).

These processes resulted intwo cultural circles forming on the territory of Georgia in the early 1st millennium BCE, a western and an eastern one, each corresponding to two unions of Georgian tribes: West Georgian and East Georgian (Janashia: 1943. 21). Hittite, Assyrian and Urartian sources reveal the most significant association ofthe Colchis (Zan) language with Kaska-Gasga and Mushkis (Meskhis) (Giorgadze: 2002, 95-113; Chitanava: 2020, 20-45). Alternatively, the development and ethnic formation of Kartvelian tribes living in the territory of modern day Georgia was an uninterrupted process (Kuftin: 1944, 47; Kuftin: 1949. 4,5).

G. Melikishvili says that Nakh-Dagestani tribes migrated from south-east Zagros, while placing Abkhazian-Adighean and Kartvelian tribes in the western regions of South and North Caucasus in the 3rd millennium BCE. He also notes that, in the same period, Iberian-Caucasian tribes, and Kartvelian tribes in particular, did not constitute a part of Kura-Araxes cultural area (Melikishvili: 1965. 23). With regard to the later epoch, the tribes that played a significant role in the formation of eastern Georgian population presumably resided in the upper reaches of Chorokhi River and territories lying east and northeast of it.

According to Strabo, Svans were strong in military affairs and had 200,000 warriors (CA: 2022-254, Strab. XI,2,19). This information, along with the Svan variant of Phasis>Pashd, led G. Melikishvili to suggest that, in the prehistoric era, the right bank of Rioni River, at least, had been settled by Svan tribes who, oppressed by Zans, were later forced to move to the highlands (Melikishvili: 1965). However, no historical documents proving that such a state ever existed have been provided.

Referring to some toponyms in west Georgia, T. Mikeladze shared G. Melikishvili’s point of view that the area around Rioni and Poti was settled by Svans before the Greeks appeared there. In his view, “Svan tribes can obviously be traced in Rioni basin, from the tributary almost to the riverheads, on the territory between Enguri and Tskhenistskhali Rivers” (Mikeladze: 1974. 11,12). He believed that a Zan-speaking population comprised an ethnic group that followed Svans and asserted that Svans lived on that territory until the mid-1st millennium BCE. However, this conclusion is based on only a handful of toponyms and cannot be regarded as strong support for this model.

Interestingly, Mikeladze developed a contrasting model in which the Colchis Bronze Age culture belongedto the Zan population (Mingrelian-Chan or Colchis), whose oppression forced Svan tribes to gradually move to the north (Mikeladze: 1974. 20). It is obvious that acknowledgement of this idea means that Svans and Zans belonged to different ethnicgroups. However, this model does not allow any time and space for the emergence of the ancestral Kartvelian language and the people who spoke it, or the gradual development of Svan, Zan and Georgian languages from a common linguistic stock. It is logical that Svan-speaking populations that formed a Kartvelian ethnic group constituted a part of proto-Colchian ethno-cultural world that extended into the Colchis Lowlands (and far beyond it). According to ancient Greek and later Byzantine sources, the name "Colchis" denominates a specific tribe as well as different Georgian tribes/communities collectively residing in west Georgia and the south-eastern Black Sea region, primarily regarded throughout antiquity as Zan (Mingrelian-Chan) tribes (Herod.VI, 79; Xenof. Anab. IV,8. 22.). The ancestors of the Svans are considered to be part of these tribes (Chartolani: 1996. 27; Mibchuani. 1989. 11, 12). It is truly stated that the population of the Kingdom of Colchis and adjacent territories were ethnically Georgian (Kartvelian) and spoke one of the west-Georgian dialects called "Colchian" by A. Shanidze, from which Mingrelian and Laz languages later appeared. Svan language originates from the same linguistic world (Gamkrelidze. 2001. 3).

Archaeology in Svaneti

The oldest archaeological sites discovered inZemo-Svanetidate to theNeolithic period. One of them is located in the Lenjeri village within the Mestia municipality, in the area called Lebikvi, at 1600 metres above sea level. Asecond one was found in Kvemo-Svaneti, near the Rtskhmelura village in theLentekhi municipality, in the area called Lazga. The Lebikvi monument represents an open ancient settlement of the 7th-6thmillennia BCE. The material discovered here stands in contrast with all the Neolithic monuments discovered in the Georgian lowlands and resembles Neolithic monuments earlier found in theSouth-West mountain front belt. In the Lebivki region, there is no human presence dating to either the Neolithic or later time period (the 5th-4th millennia BCE).Neolithic materials found at thePaluri settlement in the Tsalenjikha municipality resembles that from Lebikvi. It seems that the Lebikvi site was a temporary summer shelter of hunter-gatherers (Chartolani: 1996, 37,38; Kvitsiani, Jibladze: 2015. 43).

Mining excavations clearly appeared in Svaneti in the late 2nd millennium BCE. Excavations in the Zargashi and Lapuri Mountains have revealed the biggest mining production sites of the Bronze Age in the Caucasus, where no comprehensive studies have yet been carried out (Chartolani : 1996. 134-135).

In the 4th-3rd millennia BCE, there emergeda wide development of the Colchis Lowland. Materials from the lower layers of the settlements in this area date to the late Neolithic, while the upper layers belong to the period from the Late Bronze Age to the late 1st millennium BCE (Yessen: 1940. 108). Here, we must contend with the tradition of arranging artificial hill-like settlements, the so-called "dikha-gudzubas", in swampy areas (Khoshtaria: 1944, 207-208). They weremostly concentrated in the Colchis Lowland along the rivers or former riverbeds within the basins of Rioni and Pichori, Abasha and Noghela and Enguri-Egristkhali Rivers (Baramidze: 2011. 63). This territory has been permanently settled since the 4th-3rd millennia BCE. After this period, people left the coastline where dikha-gudzubas were mostly spread and moved to the mountains (Khoshtaria: 1945, 466-468).

One of the earliest high-output centers of copper production in Colchis metallurgy appears to have beenlocated in the basin of the Chorokhi River (Kakhide: 2000). A secondequally important metallurgical center existed in the central part of Colchis, in the interfuvium of the Rioni and Tskhenistskhali Rivers, Yet another powerful metallurgical center was located in north-west Colchis (upper reaches of the Kodori River). Earlier than in all regions of west Georgia, copper metallurgy was introduced in Abkhazia and Imereti (Kvirila gorge) in the Early Bronze Age. In Guria, Racha and Svaneti, metallurgical production of copper in the Middle Bronze Age has also been confirmed. Excavations in Mingrelia and Lechkhumi have revealed no traces of copper metallurgy earlier than the Late Bronze Age.In a multi-layer cultural site (Baksania Cave) located adjacent to a dam construction area, unique metallurgical material of the Copper and Bronze Ages was discovered in 1964. The smelter with remnants of a unique forge has no analogues on the territory of Georgia (Grigolia: 1971. 181).

Genetic Analysis of the Populations of Georgia

Our American-Georgianteam (led by Th. G. Schurr and A. Yardumian (USA) and R. Shengelia (Georgia)). began generalized genetic field research of the population of modern-day Georgia in 2012. The first research carried out in Svaneti (Mestia municipality) was followed by a corresponding publication (Yardumian et al: 2017). Subsequently, a large-scale testing of the population of Mingrelia (eight municipalities) took place (Schurr et al: 2023). These published results presented a fairly complete picture of the genetic profile of these two Kartvelian speaking populations. In addition, hundreds of samples from Guria and Adjaria as well as a similar number from Samtskhe-Javakheti are currently being analyzed. In a separate study, some ethnic and subethnic groups of east Georgia were studied (Armenian and Azerbaijani minorities, the so-called Pontic Greeks in Tsalka municipality, Tushis and a group of Fereydani Georgians whose ancestors were forced to migrate to Iran 400 years ago (Shengelia et al: 2017).

For this analysis, the principal aim of our research is to phylogenetically analyze the genetic data and assess the relationships between Svans and Mingrelians. This analysis allows us to consider their territorial distribution in a single context and evaluate the causes and timing of their language differentiation. We are focusing on Y-chromosome diversity based on evidence that the distribution of male lineagesoften reflects opulation movements and ethno-genetic differentiation (Koptekin, et al: 2023).

MATERIALS AND METHODS

Weanalyzed datafrom 17 STR loci (DYS393, DYS390, DYS19, DYS391, DYS385a, DYS385b, DYS439, DYS389a,DYS392, DYS389b, DYS458, DYS437, DYS448,Y_GATA_H4, DYS456, DYS 438, and DYS635) obtained by the American-Georgian team using the Y-Filer kit (ABI). These data were generated from 93 males in Svaneti (Yardumian, et al: 2017) and 364 males from Mingrelia (Schurr et al., 2023), as well asfrom an additional 11 Georgians and one Russian men.

Based on the data of the mentioned haplotypes, phylogenetic trees were constructed using a special program (see below) both for the Mingrelia and Svaneti populations separately, as well as using the combined (mixed) database of haplotypes from them.. This approach allowed the visualization ofthe interrelationships of the haplotypes included in this database.

Phylogenetic trees for the Mingrelian plus Svan haplotypes andthen for Svans and Mingrelians haplotypes separatelywere generated using theKilin-KlyosovTime to Most Recent Common Ancestor (TMRCA) Calculator (Klyosov and Kilin: 2016). The calculations are based on the equation: $n/N = kt$ where n =the number of mutations; N =the number of haplotypes; k =the mutation frequency constant, expressed as the number of mutations per generation; and t =the number of conditional generations (25 years).Haplotype trees were generated from Y-STR haplotypedatausing the Neighbor-Joining algorithm in PHYLIP, Version 3.6 (Felsenstein: 2004). For multiple examples of usage and calculations, see Klyosov and Kilin (2016). The correction for back mutations was estimatedusing the formula

$$\lambda = \frac{\lambda_{obs}}{2}(1+\exp(\lambda_{obs}))$$

where $\lambda_{obs}$was the average observed number of mutations per marker estimated using the formula Nm/Nh/kfm, where Nh =number of haplotypes, Nm=number of markers, Ntm=Total number of mutations;and λ is the corrected number of mutations per marker. Standard deviations (Sd) in the TMRCA, which sometimes are called “error margins”, were calculated employing common procedures, such as described below. For example, if a set of Nh haplotypes, which is proven to descend from a common ancestor, and/or belong to the same branch in a haplotype tree, contains Nm mutations from the base haplotype (which corresponds to the TMRCA equal to Tmrca ybp, with a correction for back mutations), then the standard deviation equals to the square root from Nm (equal to $\sqrt{Nm}$), then $1/\sqrt{Nm} = k$, then $(k)^2$, then adding 0.01 (this is the error margin of the mutation frequency constant) and finally taking the square root of the last value: $\sqrt{(k)^2+0.01}$, which results Sd - percent number of the TMRCA value (Klyosov: 2009.190-193). Phylogenetictrees for Mingrelians and those for Svans plus Mingrelians were analyzed separately. Analysis in this context means (a) determination of a clusterof haplotypes in the branch, and (b) determination of TMRCA for each branch. The results of these calculations are provided in Table 2.

RESULTS AND DISCUSSION

As shown in the Table 1, there was limiteddiversity of Y-chromosome haplogroups in Svaneti. This mountainous region has a highpercentage of G2a Y-chromosomes (almost 80%), which was not surprising considering the relatively isolated and closed Svan population. With regard to other paternal lineages, haplogroups, J2andR1a were present at 6.5% and9.7%, respectively, in Svans, whereas they occurred at 28.0% and 4.7% in Mingrelia, respectively. Haplogroups G1, I2, N and Q1bwere either present at low frequencies or absentfromSvans and Mingrelians and, thus, were not further analyzed for this reason. Overall, the population of Mingrelia was much more genetically diverse than that of Svaneti. This finding is likely due to its population census size, the larger number of males sampled, and its larger area of settlement.

Table 1. Y-chromosome Haplogroupsin Svaneti and Mingrelia Populations

	Mingrelians		Svans	
Hg	**n**	**%**	**n**	**%**
G2a	162	44.5	73	78.5
J2	102	28.02	6	6.5
L1b	25	6.9	0	-
J1	19	5.0	0	-
R1a	17	4.7	9	9.7
R1b	17	4.7	0	-
E1b1b	12	3.0	0	-
Q1b	5	1.4	0	-
I2	3	0.82	4	4.3
G1	2	0.6	0	-
N	0	-	1	1.00
Total	**364**	**100.00**	**93**	**100.00**

Note: The Svan dataweretaken from Yardumianetal. (2017) and Mingrelian data from Schurr et al (2023).

In what follows, we will discuss the haplotypes revealed in Mingrelia and the results of phylogenetic and coalescence analysis of the haplogroups and their sublineages that were present in the region. We then discuss the analysis of the combined data from Mingrelia and Svaneti.

Table 2. presents the calculated TMRCAsfor haplotypes occurring in either Svans or Mingrelians and alsocombined haplotypes for specific haplogroups occurringin both regions.

Table 2.Coalescence Analysis of Svan and Mingrelian Y-chromosome Haplogroups

Hg	Subclade	# Ht	TMRCA (ybp)	Basic Y-STR Ht	Notes
G2a					
	G2a1	54	3120±380	BH: 14 22 15 10 15**16 11**12 10 29 – 17 16 21 11**16**10 21	Svans only
	G2a1	19	1,575 ± 340	BH: 14 22 15 10 15 17 12 12 10 28 16 16 21 11 16 10 21	Svans only
	G2a1	112	3,860±420	BH: 14 22 15 10 15 17 12 12 10 29 – 17 16 21 11 15 10 21	Mingrelians only
	G2a1	112+54	3,680± 420	BH: 14 22 15 10 15 17 12 12 10 29 – 17 16 21 11 15 10 21	Mingrelians + Svans
	G2a2	47	4,850 ± 570	BH**:**14 22 15 10 13 14 11 12 11 29 – 17 16 21 12 16 10 21	Mingrelians only
J2					
	J2a	6	8,500 ± 1,400	BH: 12 24 15 10 14 16 13 14 11 30 17 15 20 11 15 9 22	Svans only
	J2a	17	13,260 ±1,600	BH: 12 24 14 10 12 15 12 13 12 29 16 15 20 12 16 10 23	Mingrelians only
	J2a	23	5,510 ± 640	BH: 12 23 14 10 12 15 11 14 11 30 – 17 15 20 10 16 9 23	Mingrelians + Svans
	J2a1b	52	5,470 ± 620	BH:12 25 15 10 14 15 12 13 11 30 – 17 16 20 11 15 9 23	Mingrelians only
J1					

	J1a	9	4,010 ± 575	BH:12 23 15 10 12 18 12 13 11 29 – 18 14 20 11 15 10 21	Mingrelians only
L1b					
	L1b	27	2,970 ± 420	BH: 11 23 15 10 13 17 12 13 13 30 15 16 19 10 15 10 22	Mingrelians only
E1					
	E1b	9	3,625 ± 610	BH:13 24 13 10 16 17 12 13 11 30 – 16 14 20 12 16 10 22	Mingrelians only
R1					
	R1a-Z645-Z93	9	2,670 ± 525	BH: 13 25 16 11 11 14 10 13 11 30 – 16 14 19 13 1711 23	Svans only
	R1a - Z645-293	9 + 10	2,250 ± 380	BH: 13 25 15 10 11 14 1013 11 30 – 15 14 20 12 15 11 23	Mingrelians +Svans
	R1b-Z2103	17	4920±690	BH: 12 24 13 11 11 14 12 13 13 30 16 15 19 12 15 12 23	Mingrelians only

Note: “Hg” = haplogroup; “Ht” = haplotype; “ybp” = years before present; “N/D” = not determined.

Phylogenetic Analysis

To compare the haplotypic diversity in Svans and Mingrelians, the Y-STR data were analyzed by haplogroup and also together as a complete set of paternal lineages.The haplotype data being used for this analysis are available in the Supplemental Materials and our published papers (Yardumian et al: 2017; Schurr et al: 2023).

Figure 1 presents a phylogeny of Y-STR haplotypes from all of the haplogroups present in Svans and Mingrelians. Each haplogroup is indicated by its alphanumeric label within squares. The numbers of the haplotypes are denoted at the end of each branch of the tree.

Almost all of the G2a Y-chromosomes in Svans belonged to the G2a1 subclade (Yardumian et al: 2017; Schurr et al: 2023). This is evident in the phylogenetic tree, which shows a distinct branch with G2a1 haplotypes from both Svans and Mingrelians (*Fig.*1). The other G2a branch contains only Mingrelian G2a2 haplotypes.

We also generated a separate phylogenetic tree for only Svan haplotypes to compare its topology to that of the tree with the combined datasets (Fig. 2). As indicated above, this tree is dominated by G2a haplotypes, which form the lower half of it, with all other haplogroups appearing in the upper half.

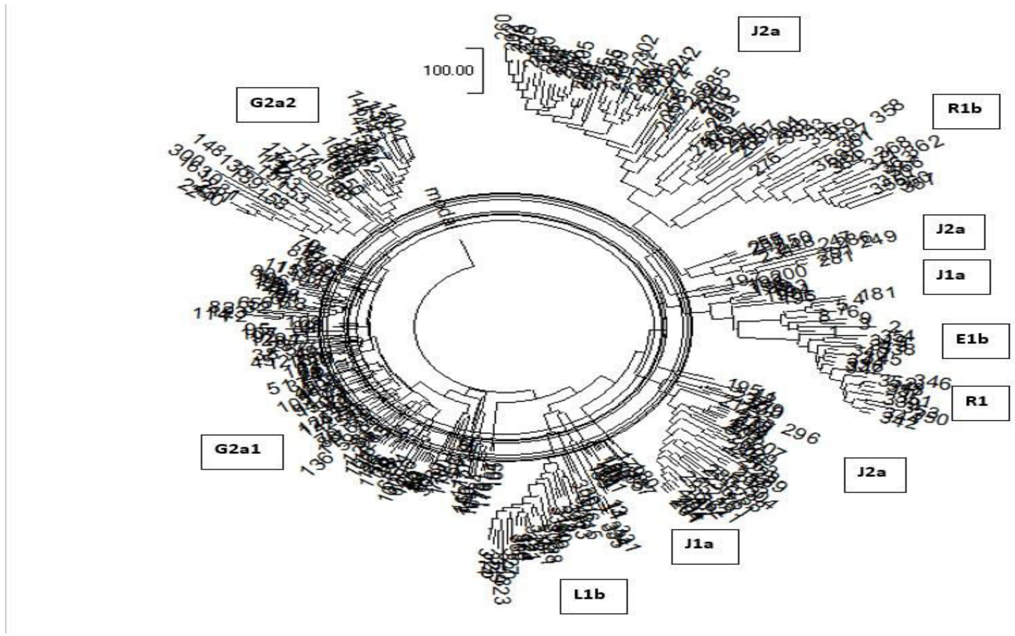


Fig. 1. Phylogenetic tree based on Y-STR haplotypes data forMingrelian and Svan populations.

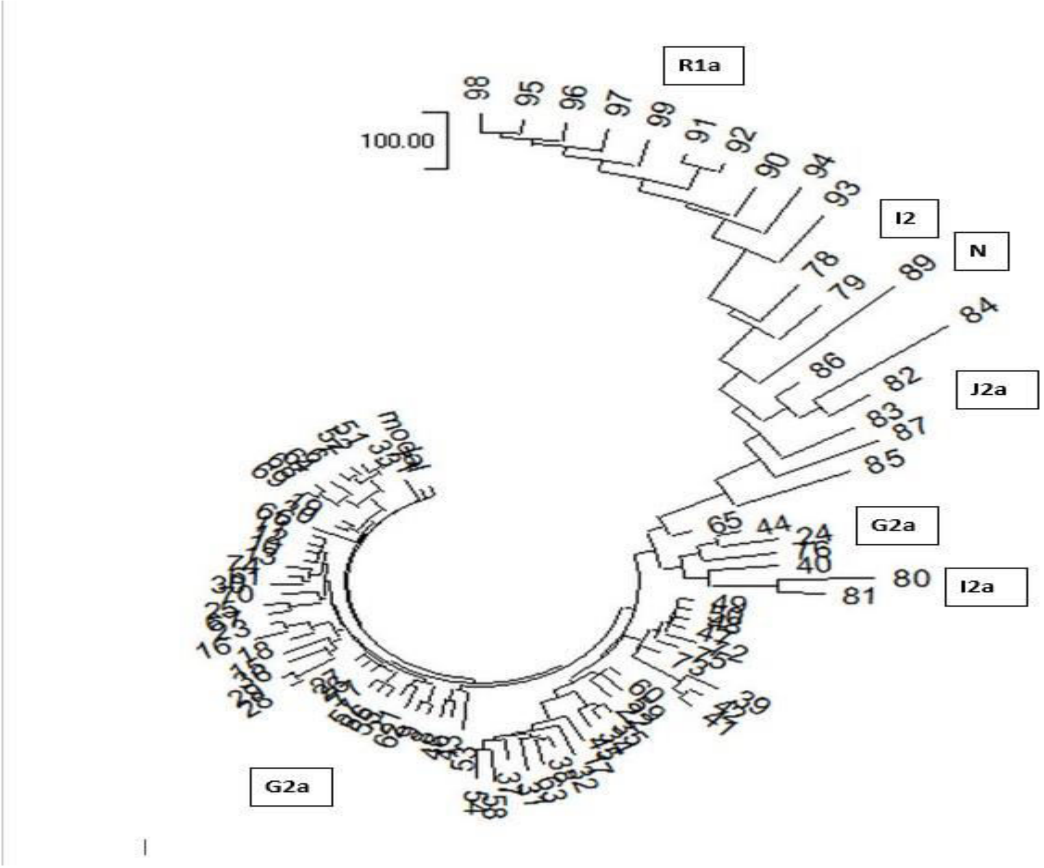
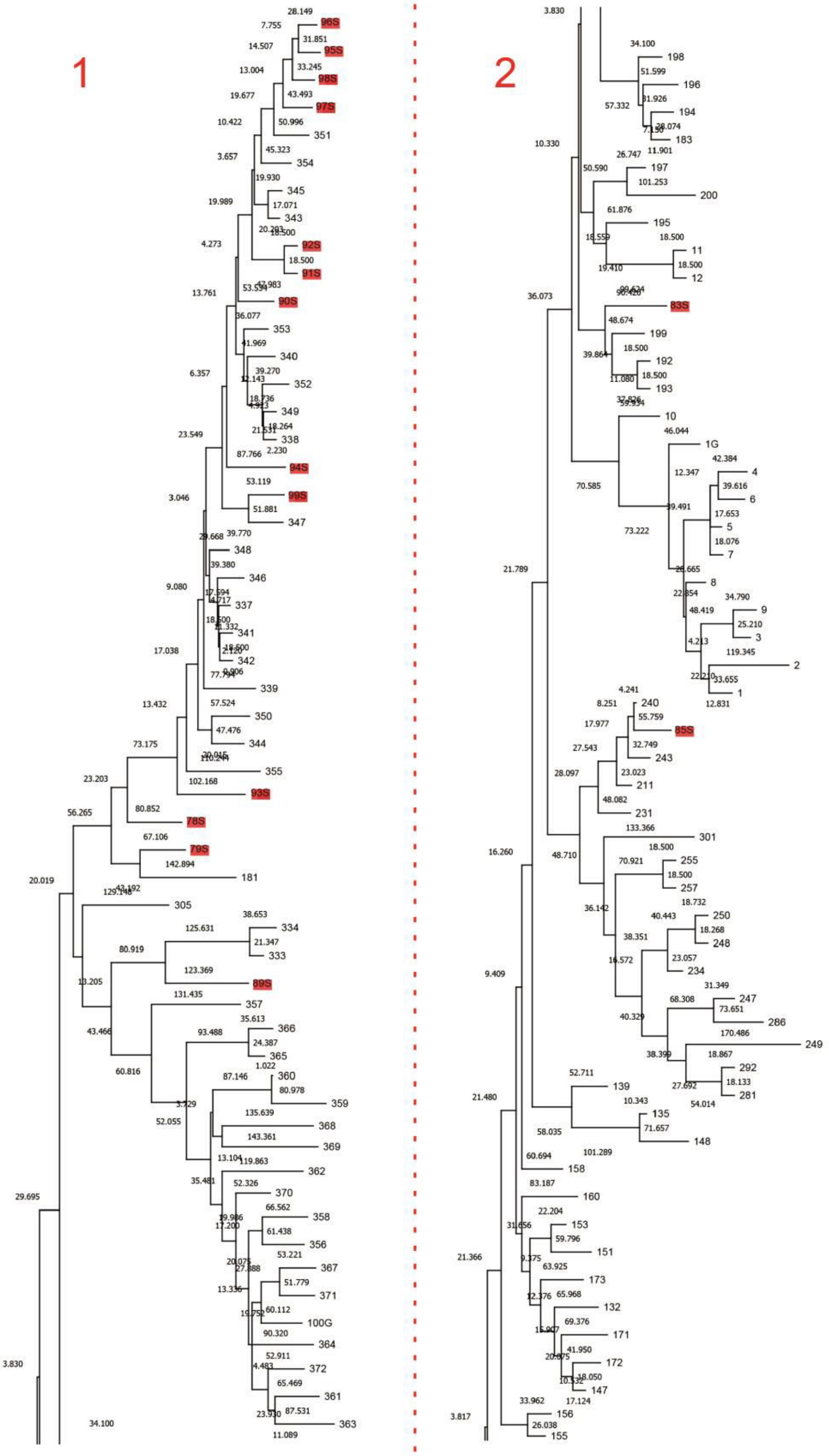


Fig. 2.Phylogenetic tree based on Y-STR haplotype data for Svan population only.

For greater clarity, we produced a linearized version of Figure 1 to show in greater detail the branching relationships among the Y-STR haplotypes used to generated it (Figure 3). In this tree, all Svan haplotypes are denoted by the letter “S” and red highlighting to distinguishing them from those occurring in Mingrelians.


1
2
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95S
98S
97S
351
354
345
343
92S
91S
90S
353
340
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99S
347
348
346
337
341
342
339
350
344
355
93S
78S
79S
181
305
334
333
89S
357
366
365
360
359
368
369
362
370
358
356
367
371
100G
364
372
361
363
198
196
194
183
197
200
195
11
12
83S
199
192
193
10
1G
4
6
5
7
8
9
3
2
1
240
85S
243
211
231
301
255
257
250
248
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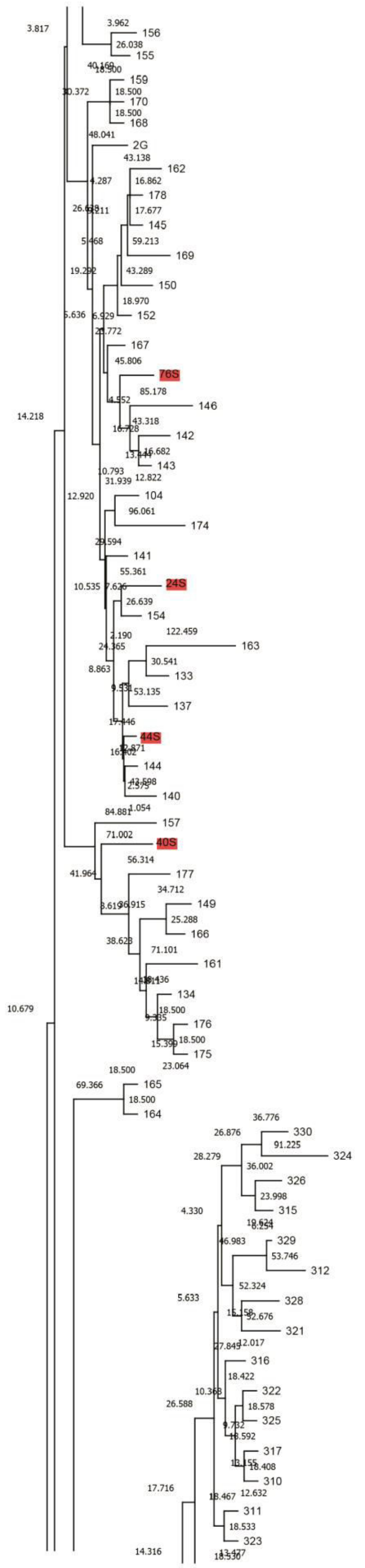
3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18.500
159
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18.500
170
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168
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2G
43.138
162
4.287
16.862
178
26.619
13.211
17.677
145
5.468
59.213
169
19.292
43.289
150
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5.636
6.929
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167
45.806
76S
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146
43.318
16.728
142
13.449
16.682
143
10.793
31.939
12.822
14.218
12.920
104
96.061
174
29.594
141
55.361
10.535
7.626
24S
26.639
154
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122.459
24.365
163
8.863
30.541
133
9.534
53.135
137
17.446
44S
16.402
2.671
144
12.698
2.373
140
84.881
1.054
157
71.002
40S
56.314
41.964
177
34.712
3.619
36.915
149
25.288
166
38.623
71.101
161
14.011
18.436
134
10.679
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18.500
176
15.399
18.500
175
23.064
18.500
69.366
165
18.500
164
36.776
26.876
330
91.225
28.279
324
36.002
326
23.998
4.330
315
19.624
8.254
46.983
329
53.746
312
52.324
5.633
328
15.158
52.676
321
27.845
12.017
316
18.422
10.368
322
26.588
18.578
325
9.732
18.592
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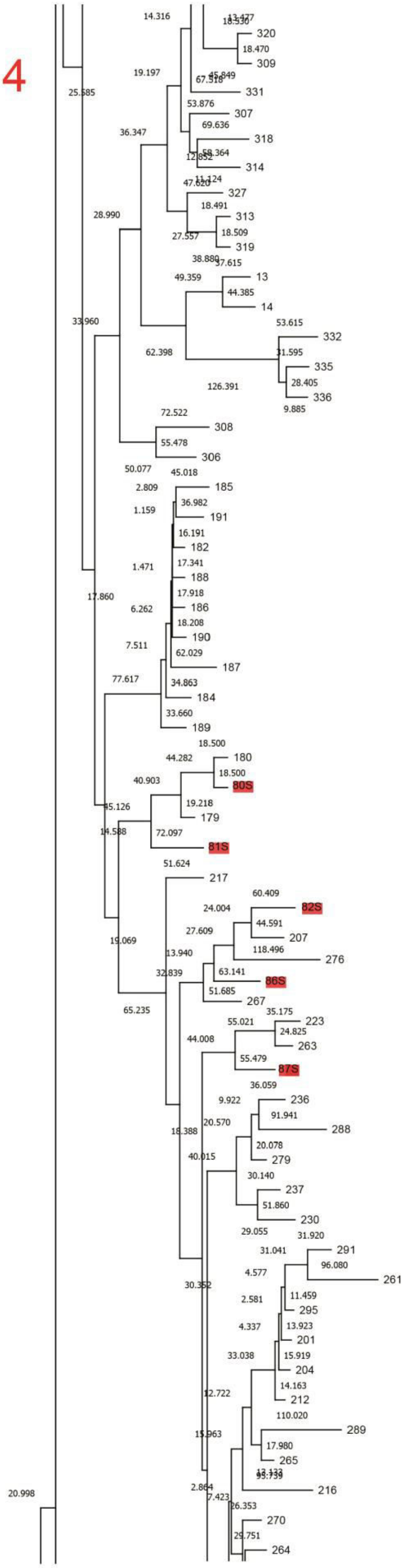
13.477
18.530

4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12.852
58.364
314
47.620
11.124
327
28.990
18.491
313
27.557
18.509
319
38.880
37.615
49.359
13
44.385
14
33.960
53.615
332
62.398
31.595
335
126.391
28.405
336
9.885
72.522
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55.478
306
50.077
45.018
2.809
185
36.982
1.159
191
16.191
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1.471
17.341
188
17.860
17.918
186
6.262
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190
7.511
62.029
187
77.617
34.863
184
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189
18.500
44.282
180
18.500
40.903
80S
45.126
19.218
179
14.588
72.097
81S
51.624
217
60.409
24.004
82S
44.591
27.609
207
19.069
13.940
118.496
276
63.141
32.839
86S
51.685
267
65.235
35.175
55.021
223
24.825
44.008
263
55.479
87S
36.059
9.922
236
91.941
18.388
20.570
288
20.078
40.015
279
30.140
237
51.860
230
29.055
31.920
31.041
291
96.080
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261
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4.337
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204
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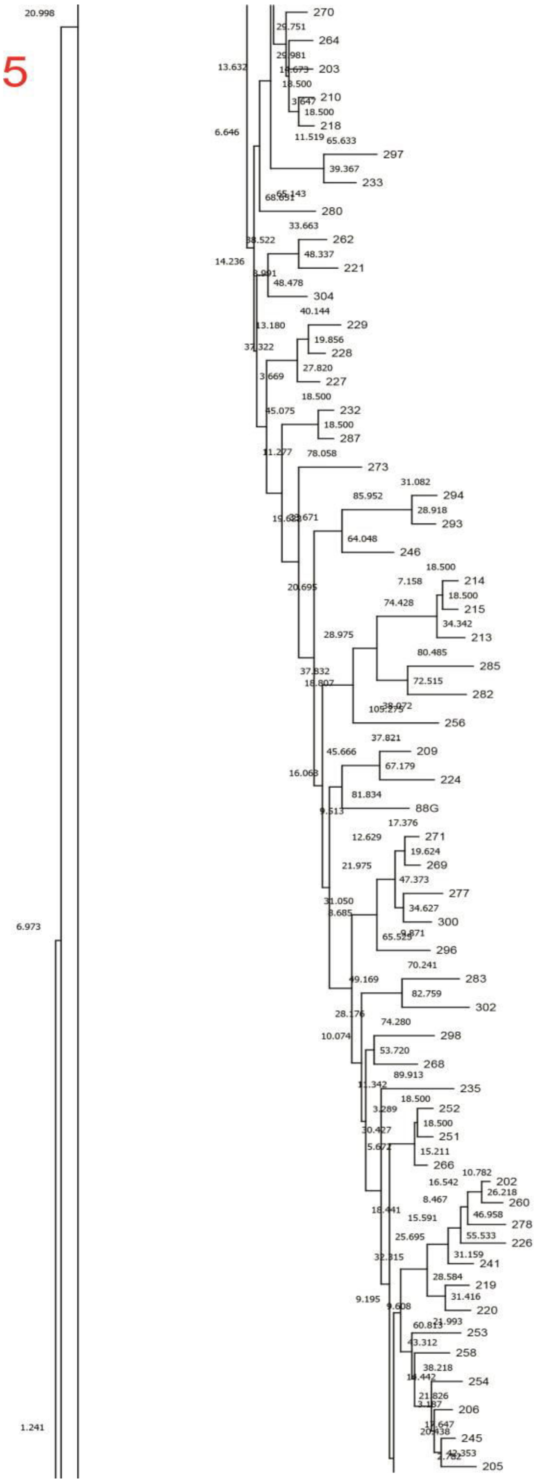
5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296
283
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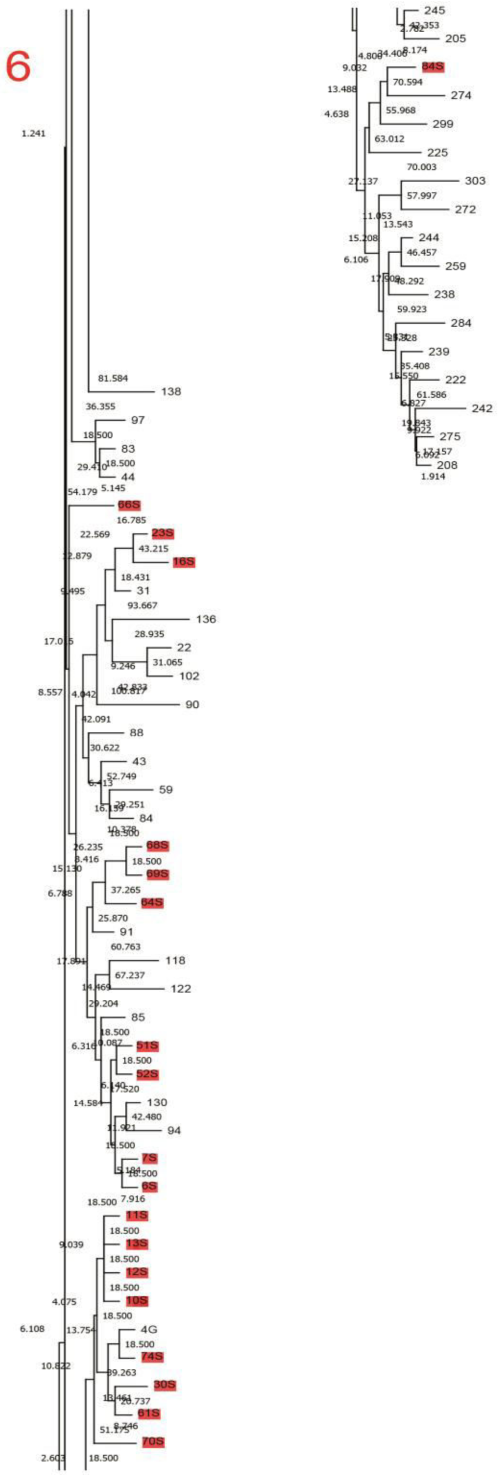
6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52S
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94
7S
6S
11S
13S
12S
10S
4G
74S
30S
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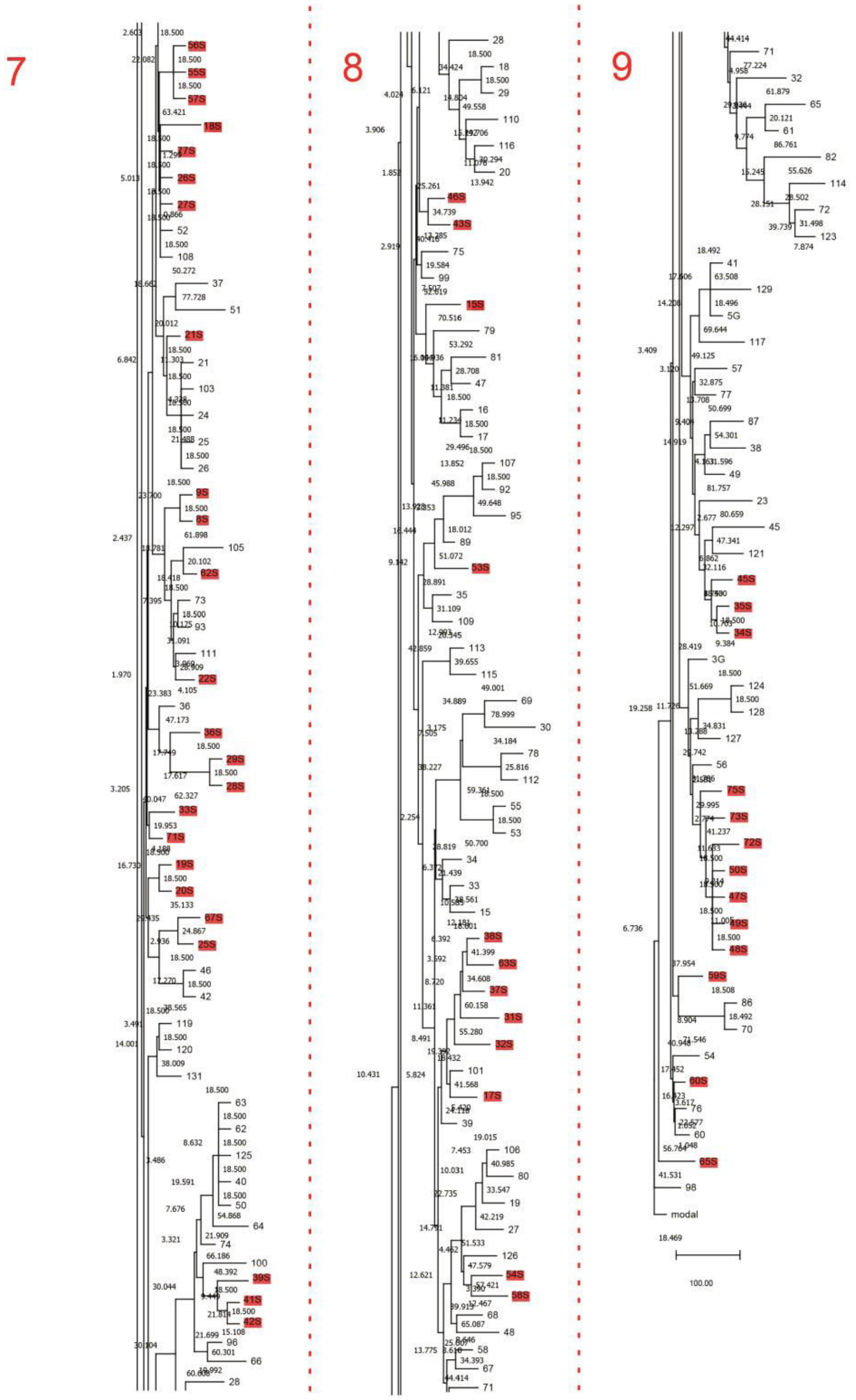

Fig. 3. An expanded phylogenetic tree of Y-STR haplotypes present in Svans and Mingrelians as shown in Figure 1. In this tree, all Svan haplotypes are denoted by the letter "S" and red highlighting to distinguishing them from those occurring in Mingrelians. The large red numbers indicate how each linearized branch shown in the tree connects to the others before and after it.

As seen in expanded form in Figure 3, there are two G2a branches. The left branch includes G2a1 haplotypes from both Mingrelians and Svans(112+54). The TMRCA for this branch was estimated to be3680± 420 ybp. The basalhaplotype for this branch has the following Y-STR allelic composition: 14 22 15 10 15 17 12 12 10 29 – 17 16 21 11 15 10 21 (see the order of the Y-STR loci above). The right branchcontains only 47 Mingrelian G2a1 haplotypes, for which a TMRCA was estimated to be4850±570 ybp. Its basalhaplotype is: 14 22 15 10 13 14 11 12 11 29 – 17 16 21 12 16

10 21. There are many Svan individuals in the left branch of G2a1, while almost no Svan individuals are represented in the lower branch (from haplotype 301 to the beginning of the right branch). The G2a2 branch differs from the G2a1 branch bynineallelic variants, indicating a considerable genetic distance between them. It translates to 9/0.0365 = 247 ± 326 conditional generations (25 years) or 8,150 years. Based on these results, it is possible thatthe ancient bearers of G2a who had a common ancestor more than 8400 years ago divided into two (future) Mingrelian branches 3900-4900 years ago. G2a Svans originated from the first branch shared with Mingrelians who lived 3680 years ago. As noted above, the second branch (4900 years) does not include Svans.

Haplogroup J2a

This haplogroupappears in the phylogenetictrees shown in Figures 1 and 3. The of Mingrelians, the upper wide double branch, while Mingrelians and Svans are represented together in the form of a large branch in the lower part of the tree.

There are only six J2a haplotypes in Svans and they are scattered throughout the long part of the branch. Their common ancestor is estimated to evolved 8500±1400 ybp. Presumably, separate individuals appeared in Svan population.

J2a haplotypes are more widespread among Mingrelians. The first (upper) branch includes 52 haplotypes with a TMRCA of5470±620 ybp and the base haplotype: 12 25 15 10 14 15 12 13 11 30 – 17 16 20 11 15 9 23. The second (lower) branch consists of 42 haplotypes with a TMRCA of 5510±640 ybp and the base haplotype: 12 23 14 10 12 15 11 14 11 30 – 17 15 20 10 16 9 23.

Thefirst branch differs from the second by 10 mutations. This differencetranslates to 10/0.0365 = 274±374 conditional generations, or 9350 years between their common ancestors. Since the common ancestor of the second branch evolved 5510±640 ybp, thecommon ancestor for both branches arose(9350+5470+5510)/2 = 10,200 years ago (a rounded figure). In other words, we see two groups of Mingrelian haplotypes, different in their TMRCA within the same J2a group. It should be emphasized, that the first (top) branch comprises J2a1b haplotypes and the second one only J2a haplotypes.

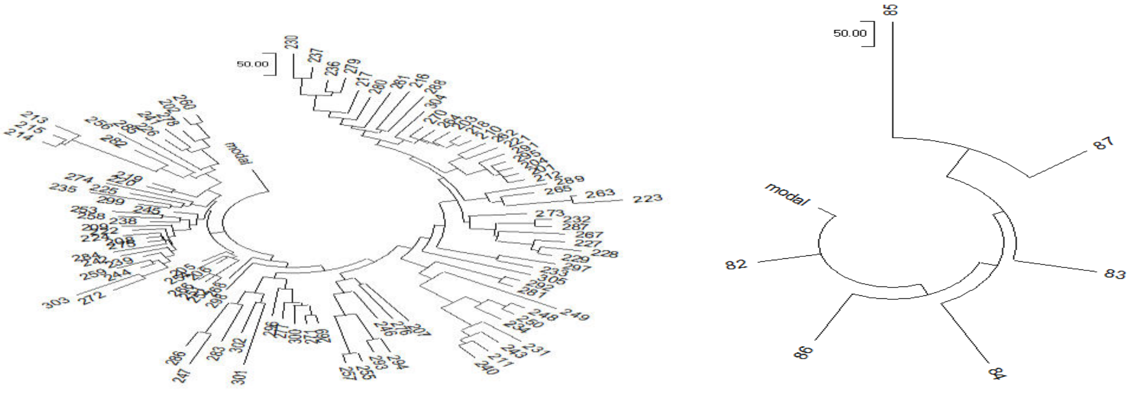

Fig. 4. Phylogenetic trees for haplogroup J2a haploptypes. The tree for Mingrelians appears on the left and that for Svans on the right.

Haplogroup R1a

A total of 19 Mingrelian and 9 Svan haplotypes belong to this haplogroup. They were phylogenetically analyzed separately to assess their evolutionary history (Figure6). Mingrelians only had the basal haplotype13 25 15 10 11 14 10 13 11 30 – 15 14 20 12 15 11 23, with its TMRCA being estimated at 2120±360 ybp (Table 2).By contrast, the Svans only had the basal haplotype: 13 25 16 11 11 14 10 13 11 30 – 16 14 19 13 17 11 23, with aTMRCA estimated to 2670±525 ybp. Overall, these results suggest that J2a haplotypes in Svaneti and Mingrelia may be related to the same historical period or source.

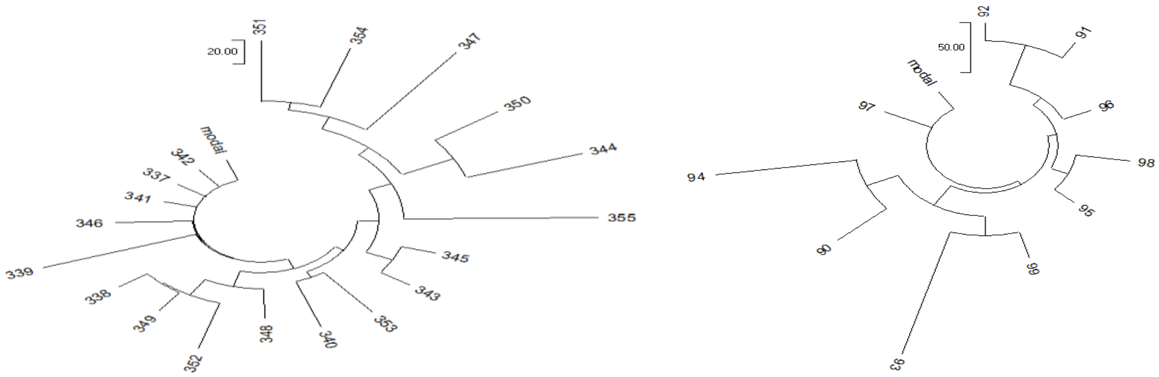

Fig. 5. Phyolgenetic trees for haplogroup R1a haploptypes. The tree for Mingrelians appears on the left and that for Svans on the right.

Haplogroup R1b

Haplogroup R1b haplotypes occurred only in Mingrelians, with the phylogenetic tree for them being shown in Figure 7. These haplotypes may have been spread into the South Caucasus by the expanding the Yamnaya steppe culture. The 17 Mingrelian haplotypes have a TMRCA of 4920±690 ybp, a date which falls within with the epoch of the Yamnaya culture(5300-4600 ybp) (Skourtanioti et al.: 2024).

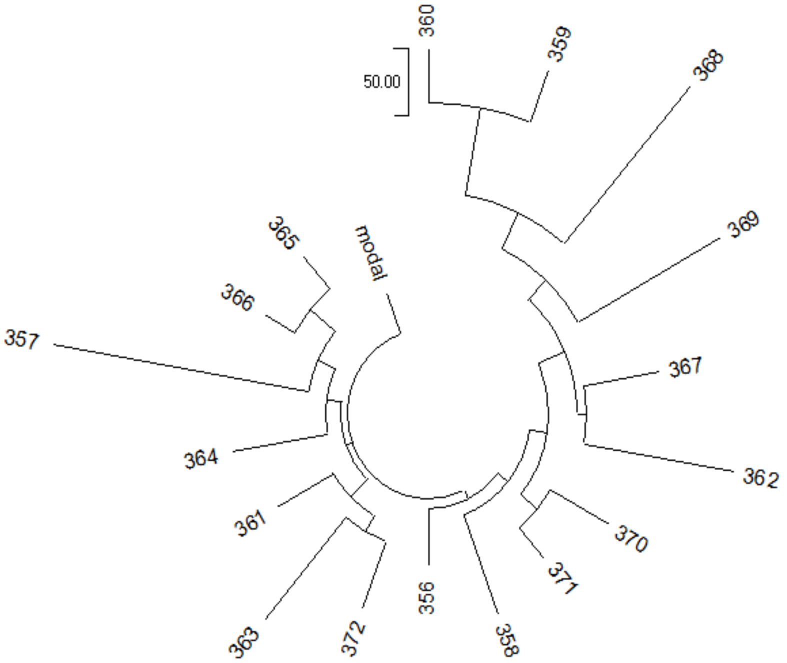

Fig. 6. Phylogenetic tree for haplogroup R1n haploptypes.

Haplogroup J1a

Haplogroup J1a haplotypes occurred only in Mingrelians and are shown in a phylogenetic tree in Figure 8. The 19 haplotypes in Mingrelian haplogroup J1a had a TMRCA of 4010±575 ybp. The basal haplotype was: 12 23 15 10 12 18 12 13 11 29 – 18 14 20 11 15 10 21. This haplotype is similar to those appearing in Chechens, Avars, Dargins and Armenians but differs from those appearing in SepharicJews(Klyosov: 2021).

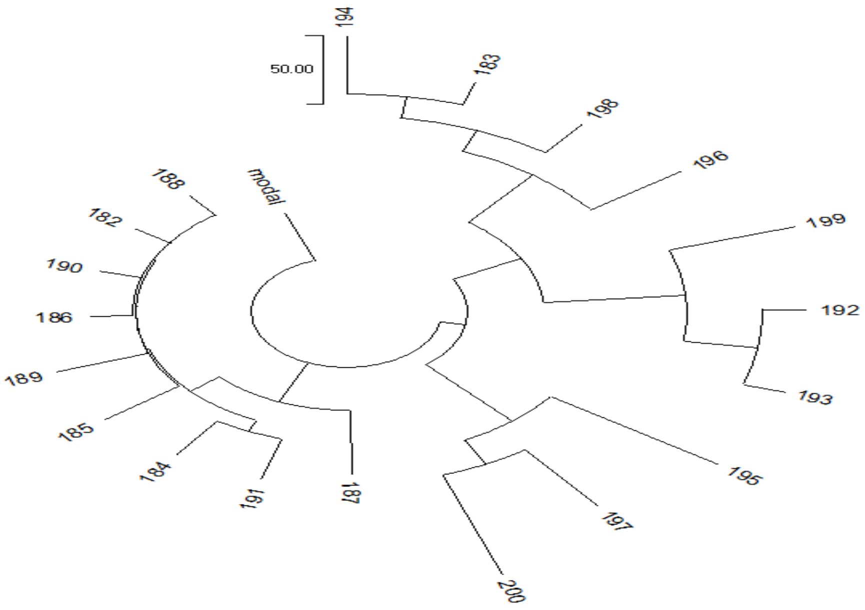

Fig. 7. Phylogenetic tree for haplogroup J1a haplotypes.

Haplogroup E1b

Haplogroup E1b occured only in Mingrelians. The 12 E1b haplotypes are shown in a phylogenetic tree in Figure 9. The basal haplotype is 13 24 13 10 16 17 12 13 11 30 – 16 14 20 12 16 10 22, with the TMRCAfor this haplogroup being dated to3625±610 ybp. This basal haplotype is somewhat similar to one appearing in Serbs (13 24 13 10 16 18 11 13 11 30 – 16 14 20 11 16 10 22; Klyosov, 2021: 653)that belonged to E1g, which has a TMRCA of2840±480 ybp. In addition, the basalE1bhaplotype for all European populations appears to be 13 24 13 10 16 18 12 13 11 30 – 15 14 20 11 17 10 22 (Klyosov, 2021, 126), for which a TMRCA of 3450±350 ybp has been estimated. It is likely that the ancestor common to these haplotypesarose about 4700 ybp (Klyosov: 2021. 464-491),

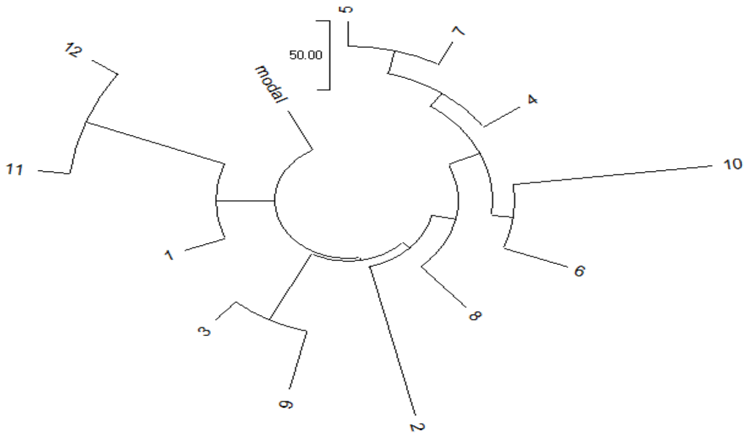

Fig. 8. Phylogenetic tree for haplogroup E1b haplotypes.

Haplogroup L1b

Haplogroup L1b haplotypes only appear in Mingrelians. A total of 27 haplotypes were identified and are shown in a phylogenetic tree in Figure 10. Its basal haplotype is: 11 23 15 10 13 17 12 13 13 30 15 16 19 10 15 10 22. The TMRCA for this lineage is 2970± 420 ybp.This is a very interesting haplogroup, and the question of its origin and distribution should become a subject of special research.

Fig. 9. Phylogenetic tree for haplogroup L1b haplotypes.

CONCLUSIONS

Comparison of the results of the phylogenetic (DNA genealogy) research carried out among the population of northwest Georgia with historical, archaeological and linguistic data revealed a number of details about Georgian population history.

First, the results of our previous studies revealed that Georgian populations presumably emerged in the form of a separate gene pool in the Early Bronze Age (4thmillennium BCE) and influenced further expansion of populations in this region (Yardumian et al: 2017). The revealed genetic variation support the significance of the geography and the critical role of the settlement phases in Caucasian highlands. They may also reflect social and cultural characteristics of the region. High frequency and diversification of G2a haplogroup of Y-chromosome solidifies the notion that itemerged *in situ* (Schurr, et al: 2023).

The present research also provides an estimate for the TMRCA of ancient haplogroup J2a revealed in Mingelia around 13260±1600 ybpwhich is quite widespread in entire population (17 haplotypes, 4.67% of the research material). Together with the results of archeogenetic studies of the individuals found in the karstcaves of Zemo Imereti, it suggests continuous residence of bearers of haplogroup J on the territory of west (and not only west) Georgia at least from Mesolithic period.

The next generations of the population of Svaneti seem to have separated from the common Kartvelian genetic stream in the Late Bronze Age, which is proved by archaeological data. The formation of Svan language had to begin in the same period. Geographic, landscape, climatic and administrative-political isolation as well as North Caucasian impact (immediate neighborhood uponthe population who spoke Abkhazian-Adighe language and Karachay-Balkar dialect of Turkic) played role in the formation of this language.

Thanks to its isolation, Svan language has preserved unique lexical and grammatical forms of the common Kartvelian language, including Anatolian and Middle Eastern parallels.In the periods to follow, the growingSvan population constantly expanded to the southwest in the direction of Mingrelia and other Georgian provinces, as well as in the direction of North Caucasus countries. Traces of Svans (toponymic, anthroponomic, ethnographic) can be revealed in the regions of present-day Balkaria, Karachay, Kabardia and central North Caucasus.

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