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Abstract

This study investigates the genetic diversity and ethnohistory of Svaneti and its neighboring highland Georgian and breakaway regions in order to better understand the complex population history of the South Caucasus. The objectives of this project are to (1) document the biological diversity in contemporary settlements in the region of Svaneti; (2) compare patterns of gene diversity with Svaneti's western and eastern neighbors, Abkhazia and South Ossetia, respectively; and (3) determine whether gene frequencies in Svaneti are evenly distributed across geographic space by characterizing any village-level structuring. We will contextualize the findings within broader studies that address major regional population settlement events during the Upper Paleolithic, Neolithic, and Metal Ages, as well as the putative 'Alan migration' in the 4th century AD. To accomplish these goals, biological samples were collected from participants in Svaneti for genetic analysis, providing a more thorough coverage of village districts in Svaneti than has been achieved in previous studies. In addition, local-level ethnohistorical interviews were conducted in an effort to distinguish patterns of diversity resulting from long-term inhabitation versus those arising from recent immigration into the region. These DNA samples were characterized for mitochondrial DNA and Y-chromosome variation, and the resulting data analyzed with statistical and phylogenetic methods to define the biological affinities of highland Georgian populations, and reconstruct the migration and settlement history of the region. Data from published and unpublished sources on the genetic diversity of the greater Near East and Caucasus, specifically Abkhaz and Ossete populations, were used for phylogeographic and statistical comparison. The results revealed reduced Y-chromosome haplogroup diversity in Svans, with a predominance of G2a, although their paternal lineages occurred at frequencies comparable to those of neighboring highland populations. By contrast, mtDNA haplogroup diversity in Svans was both very high and reasonably similar in terms of frequency to other regional populations, with W6 and X2 occurring at unusually high frequencies. Interestingly, there was no geographic patterning of Y-chromosome or mitochondrial DNA diversity within Svaneti at the village level. Nevertheless, strong Y-chromosome affinities with eastern and western populations (i.e., Ossete and Abkhaz, respectively) living adjacent to the Svans indicated a common gene pool for these three ethno-linguistic groups in spite of linguistic differences at the language family level, and minimal contribution to the Ossete gene pool from Indo-European-speaking Alans.

Degree Type

Dissertation

Degree Name

Doctor of Philosophy (PhD)

Graduate Group

Anthropology

First Advisor

Theodore G. Schurr

Keywords

Caucasus, Haplogroup, Svaneti

Subject Categories

Biological and Physical Anthropology | Genetics | History of Art, Architecture, and Archaeology

GENETIC DIVERSITY IN SVANETI AND THE HIGHLAND WESTERN CAUCASUS

Aram Yardumian

A DISSERTATION

In Anthropology

Presented to the Faculties of the University of Pennsylvania

in

Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

2015

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GENETIC DIVERSITY IN SVANETI AND THE HIGHLAND WESTERN CAUCASUS

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კუძლწნი გორგი ქავთარაბე
and to my stepfather, Gerald Hurst

ABSTRACT

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Aram Yardumian

Prof. Theodore G. Schurr

This study investigates the genetic diversity and ethnohistory of Svaneti and its neighboring highland Georgian and breakaway regions in order to better understand the complex population history of the South Caucasus. The objectives of this project are to (1) document the biological diversity in contemporary settlements in the region of Svaneti; (2) compare patterns of gene diversity with Svaneti's western and eastern neighbors, Abkhazia and South Ossetia, respectively; and (3) determine whether gene frequencies in Svaneti are evenly distributed across geographic space by characterizing any village-level structuring. We will contextualize the findings within broader studies that address major regional population settlement events during the Upper Paleolithic, Neolithic, and Metal Ages, as well as the putative 'Alan migration' in the 4th century AD. To accomplish these goals, biological samples were collected from participants in Svaneti for genetic analysis, providing a more thorough coverage of village districts in Svaneti than has been achieved in previous studies. In addition, local-level ethnohistorical interviews were conducted in an effort to distinguish patterns of diversity resulting from long-term inhabitation versus those arising from recent immigration into the region. These DNA samples were characterized for mitochondrial DNA and Y-chromosome variation, and the resulting data analyzed with statistical and phylogenetic methods to define the biological affinities of highland Georgian populations, and reconstruct the migration and settlement history of the region. Data from published and unpublished sources on the genetic diversity of the greater Near East and Caucasus, specifically Abkhaz and Ossete populations, were used for phylogeographic and statistical comparison. The results revealed reduced Y-chromosome haplogroup diversity in Svans, with a predominance of G2a, although their paternal lineages occurred at frequencies comparable to those of neighboring highland populations. By contrast, mtDNA haplogroup diversity in Svans was both very high and reasonably similar in terms of frequency to other regional populations, with W6 and X2 occurring at unusually high frequencies. Interestingly, there was no geographic patterning of Y-chromosome or mitochondrial DNA diversity within Svaneti at the village level. Nevertheless, strong Y-chromosome affinities with eastern and western populations (i.e., Ossete and Abkhaz, respectively) living adjacent to the Svans indicated a common gene pool for these three ethno-linguistic groups in spite of linguistic differences at the language family level, and minimal contribution to the Ossete gene pool from Indo-European-speaking Alans.

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CHAPTER ONE: THE HIGHLAND NORTHWEST CAUCASUS

Ia. Aims of the Project

This dissertation emerges from a proposed study to investigate population histories in Georgia, the purpose of which is to situate populations within Georgia in a genetic and historical descriptive framework for reconstructing the migration and settlement of ancient Eurasian peoples. The data collected and described herein represents the first dedicated genetic description of the Svans.

This dissertation, as well as its parent Georgian Genetic History Project, will complement similar recent work (e.g., Balanovsky et al. 2011; Herrera et al. 2011; Yunusbayev et al. 2012) that has compared the linguistic and genetic affinities of Caucasus populations. The foremost of these has noted the parallel evolution of languages and genes among four ethno-linguistically affiliated populations (including Abkhaz and Ossetes) in the North Caucasus. This dissertation will extend this manner of research over the mountain barrier into the South Caucasus highlands. Yunusbayev et al. (2012) have suggested the Caucasus Mountains are semi-permeable by humans, and thus have served to limit gene flow across them. The data in this dissertation do not devalue this assertion—in a certain sense, they confirm it—but also make a case for a very different kind of demographic process in the South Caucasus than that depicted by Balanovsky et al. (2011) and Yunusbayev et al. (2012) in the North.

Although situated in close proximity to the highlands in and around northwestern Georgia, the populations of Abkhazia, Svaneti, and Ossetia (both North and South) have divergent linguistic affiliations and historical traditions of origin. A

few genetic studies of these populations have been published in the last two decades. Abkhaz and Ossete Y-chromosome data appeared in Balanovsky et al. (2011) and Ossetian mtDNA and Y-chromosome data were published in Nasidze et al. (2004b) and Nasidze (2008). Unfortunately, Abkhaz mtDNA data are lacking. Three studies that featured small Svan data sets are Sánchez-Velasco and Leyva-Cobián (2001), Wells, et al. (2001) and Alfonso-Sánchez et al. (2006). None of these studies proposed or attempted to investigate genetic affinities between Abkhazia, Svaneti, and Ossetia, and until now Svaneti has remained largely genetically undescribed. Although several other regions within Georgia remain unsampled, the reason for the absence of data from Svaneti may be related to its historical lawlessness, a situation remedied only in recent years (*s.n.* 2004).

Ib. The Geography and History of Svaneti

The geographic isolation of Svaneti has lent much to its mythical status as a place inhabited by an ancient and autochthonous people. Situated in the upper valleys of the Inguri, Rioni, and Tskhenis-Tsqali Rivers, in a land of alpine meadows and forests, the region until very recently was only accessible by poorly maintained roads and riverine trails. The Great Caucasus peaks divide it from its North Caucasus neighbors, Karachay-Circassia and Kabardino-Balkaria, to which passage is possible along a few foot and horse paths. To the west is Abkhazia, a Black Sea coast breakaway region whose language clusters with Abaza, Adyghe, Circassian, and the extinct Ubykh to form the Northwest Caucasian family (Chirikba 2008: 29). To the east

and southeast are the Georgian provinces of Racha and Lechkhumi, which have also been sporadically inhabited by Svans, and to the south is Mingrelia (**Figure 1**). Beyond Racha to the east lies South Ossetia, a breakaway region from Georgia's Shida Kartli district. Although these regions are today accessible by paved roads, the two breakaway regions have been closed from the Georgian side since 1992 (Ossetia) and 1994 (Abkhazia), respectively (see Hewitt 2013), with the Georgian-'Ossetian' border being established only years after the war by Russian troops (Kevorkova 2013). Svaneti itself is now more easily accessible to Georgian vehicle transit than ever before in its history of rough terrain, periodic political fragmentation (Гасвиани 1980: 64-65, 81-83) and blood feud politics (Гасвиани 1980: 57-61).



Figure 1. The administrative districts of Georgia (www.bonafide.ge)

Svaneti is divided into two geographic parts, Lower Svaneti (or Kvemo Svaneti) and Upper Svaneti (Zemo Svaneti). Lower Svaneti is grouped with Racha and Lechkhumi into a unified administrative unit separate from Upper Svaneti, which is grouped with Samegrelo into a unit called Samegrelo-Zemo Svaneti (**Figure 2**). Upper Svaneti is, in turn, divided by the Bal mountain range into two parts, Upper Bal and Lower Bal. Throughout the centuries, the regions of Upper Svaneti have shifted allegiances and modes of suzerainty with fragments and fissions, allegiances and confederations, occasionally leading to breaks with the central government (Гасвиани 1980: 88-90). In fact, during much of the 18th and 19th centuries, Upper Bal, or 'Free Svaneti', existed entirely without nobility or serfdom (Авалиани 1913: 45-59). In spite of their independence and isolation, Svans have long depended on remittances from migrant labor performed in lowland Georgia. Their cultural interdependence has also been reinforced by the authority of the Georgian Orthodox Church, to which most Georgians belong (Гасвиани 1980: 19, 26).

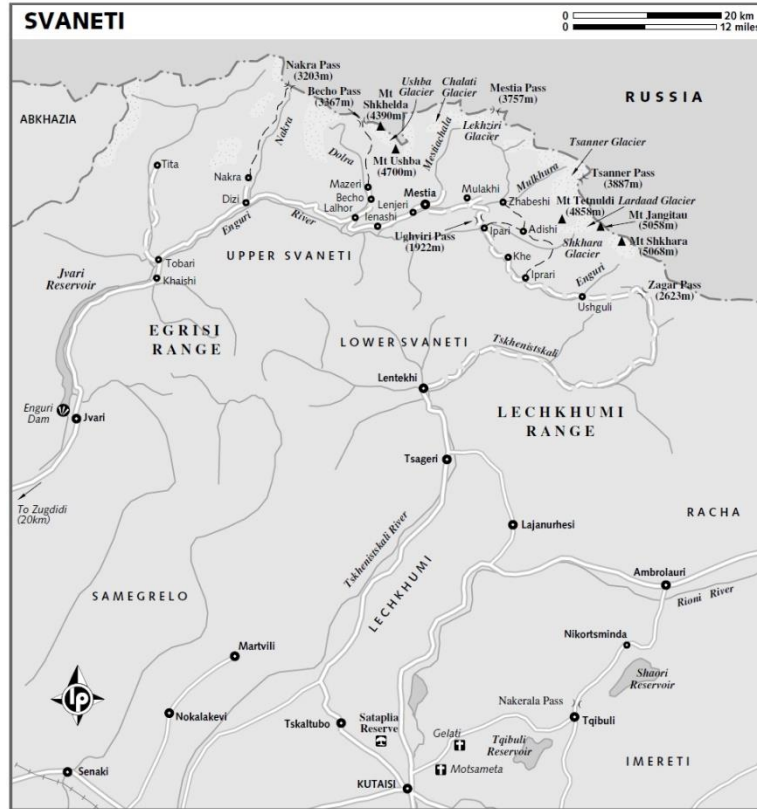


Figure 2. A map of Svaneti (<http://eurasia.travel/georgia/places/mountains/svaneti/>)

Although scattered scrapers and blades attest to sparse Neolithic settlement in the Svaneti region (Բართოლანი 1996), it is with the presence of copper spearheads and axes (some supposedly with Kura-Arax affinities) which begins a period of cultural continuity in Svaneti continuing through the Iron Age and into Antiquity (Բართოლანი 1996). While pre-Neolithic sites are not yet known in Svaneti, it lies along two natural trans-Caucasus corridors between western Georgia and the Russian steppe. Thus, like Daghestan, it is positioned perfectly for studies of long-term habitation and migration in the Caucasus region.

The Svan speech community numbers around 35,000 to 40,000, inclusive of diaspora communities within Georgia (Tuite 1995)¹. The Svan language is mutually unintelligible with other Kartvelian languages, sharing a mere 360 lexemes with Georgian and 340 with Zan (Laz and Mingrelian), while the latter two (Georgian and Zan) share 825 lexemes (Klimov 1969). This difference, in addition to a highly divergent morphology, especially in matters of vowel inventories and suffixation, situates Svan as the farthest outlying member of the Kartvelian family (Deeters 1930; Schmidt 1962, 1989; Tuite 1995, 1997). Among the Kartvelian languages, Svan is distinct (though not unique among the four) for its accrual of vocabulary from neighbors across the Caucasus, particularly, according to Tuite (1995: 2), speakers of Northwest Caucasian languages, which would include Abkhaz. Its shared vocabulary with Circassian and Kabardian includes words for different kinds of flour and other aspects of agriculture, among many others. Svan also shares words for kinds of flour with Chechen-Ingush (although different terms from those shared with Circassian and Kabardian), as well as the name of the goddess of game animals and the hunt. These terms are quite basic and indicative of longstanding contact, while the mutual unintelligibility with Georgian is indicative of longstanding isolation of the Svan speech community from Georgia at large.²

¹ ზანდუკიძე (1967: 162) reports an unpublished government document from 1909 that puts the Svan population of Upper Bal in that year at 11,896, of whom 1,646 had applied to the police for passports.

² Whether or not Svan is a creole, hybrid, or otherwise mixed, language, drawing on Kartvelian and Abkhazo-Adyghean languages (see Чикобава 1948a; ჯანაშია ს. 1942; თოფურია 1931), remains an open question, but one which resulted in a decades-long pre-War debate among Georgian Kartvelologists. Spirited as the debate became, its participants agreed on two principles, as formulated by Marr (1911), namely, that (1) all of the indigenous Caucasian languages were genetically related, and that (2) a diversity of speech varieties and ethnic communities, from both sides of the Caucasus, contributed to the

Svan is further subdivided into four mutually intelligible regional dialects, Upper Bal, Lower Bal, Lentekhi, and Laskh (sometimes Saqdar is considered a fifth) (Tuite 1997: 1). However, vowel inventories differ even between the dialects of Svan (Tuite 1995: 3). According to Tuite (1995: 2), until the 19th century, most Svans were monolingual aside from migrant laborers, traders, and those living on the geographic borders of other speech communities (i.e., Georgian, Mingrelian or Balkarian). This fact has lent something to Svaneti's reputation as both a culturally, and perhaps biologically, isolated community. Its reputation as a historical refuge from long civil wars and foreign invasions (especially Mongol and Ottoman, the former of which thoroughly ravaged much of lowland Georgia) (Lang 1955; Suny 1994: 39-44) has enhanced this reputation. During Mongol incursions into the South Caucasus in the 13th century, for example, Svaneti's churches served as hiding places for Georgia's secular and religious artistic heritage (e.g., icons and illuminated manuscripts, as well as gold and silver items) (Tuite 2007).

Despite periodic isolation, and the perseverance of a linguistic identity that this isolation may have helped forge, Svaneti has, in fact, long served as a mediation point for trade between the North Caucasus and lowland Georgia. According to Гасвиани (1980: 80), Svans traded goods (presumably honey, lead, iron, felt and wool, perhaps even calico) with the peoples of Karachay-Circassia and Kabardino-Balkaria, and probably sold them at a premium in Mingrelia. Topographically, Svaneti is unsuited to

emergence of Svan. The debate pivoted on the socio-historical mechanism(s) to which the hybrid nature of Svan could be attributed, whether (1) intensive areal contact, (2) the spread of Kartvelian languages into the territories of Abkhazo-Adyghean language-speakers, or (3) the 'radically autochthonist explanation favored by Marr in his later years' (see Tuite 2011: 11-12).

sustainable agriculture, and thus regular economic relations between it and lowland Georgia are a long established tradition, serving not only as a transit service for goods, but as a source of cheap manpower for wages in the lowlands. Thus, as it has been said: ‘An able-bodied Svan is the guest of his own family. Three quarters of the year he lacks in his hearth, for in autumn and winter he works in Mingrelia for a trifling sum’ (გელოვანი 2003: 162).

Between the disintegration of the Georgian Kingdom in the 15th century CE and the present, Svaneti changed hands between various small fiefdoms, kingdoms, and empires. However, not until the abolition of serfdom in 1871 is there evidence for an important demographic shift there. At this time, all peasants were freed and given a small plot of land, albeit often so small they were forced to rent more, again, from the nobility (Авалиани 1913: 46-50; Suny 1994: 109). The feudal system, especially its dissolution and its restructuring of land tenure, very likely shuffled a very old clan-based system in which certain families claimed residence in their home village since the 11th century or before (Гасвиани 1980). Soviet resettlement activities in the Caucasus seem to have had no effect on clan distribution and overall population dynamics in Svaneti.

Svans are partially endogamous as a population, if only because Georgian lowland women rarely married into highland families, and given that Svan women are more willing to marry Georgian lowlander men (Topchishvili 2005). The *samkhub*, or clan, generally resides within a single village, and land owned by a clan is distributed to constituent family groups. When this land is alienated, it is preferentially given to close

patrilineal relatives, with the result being that patrilineages can reside on a physical plot of land for many generations. Indeed, the separation of brothers from their household after the death of their father was highly discouraged, making males further attached to the land on which they were born. By contrast, wives were traditionally taken from another *samkhub*, establishing women as geographically mobile in relation to their particularly immobile male counterparts (Tuite 1994). In the past, marriage within the *samkhub* or with other relatives within ten degrees of kinship was considered taboo (Tuite 2007).³

Based on linguistic and ethnographic evidence, Svaneti would seem to be a historically isolated region, although one not entirely inaccessible. However, such a statement cannot resolve questions as to whether the Svan population and its neighbors (e.g., Abkhaz, Ossetes, non-Svan Georgians, Armenians) form separate bio-linguistic zones, as is the case in the North Caucasus (e.g., Balanovsky et al. 2011), or whether their social formations stem from a more complex set of lineages. Furthermore, there is the longstanding question about the geographic origin(s) of Kartvelian languages, and the impact of Kartvelian-speakers on settlement patterns in the South Caucasus.

Kavtaradze (1985, 2000), and ჯავახიშვილი (1950) and von Klaproth (1831) before him, situate the Kartvelian Urheimat in eastern Anatolia and the Ararat Plains. Kavtaradze (2000) makes the case beginning with the observation that the substratum language for both Hittite (an Indo-European language) and Hattic (an unclassified Anatolian language isolate, known only indirectly from Akkadian, Assyrian, and Hittite

³ While in Mestia, our team visited a local record-keeper who pledged to provide the project with copies of Svan genealogical records for analysis. However, these copies have yet to be prepared.

textual sources; Bryce 2005) is probably Kartvelian (Drews 1988; Ehret 1988; Houwink ten Cate 1995; McMahon 1995; Zimmer 1990). Kavtaradze (2000) also notes that there are strong and established lexical parallels between the existing Hattic corpus and the languages of northwest Caucasus (i.e., Abkhaz and Circassian) (ИВАНОВ 1985). In addition, the Hittite-Armenian lexical parallels are of a distinctly non-Indo-European character, while there are also strong lexical parallels between the Hurro-Urartian languages and the northeast Caucasian languages (i.e., Chechen, Ingush, Avar) (Diakonov 1990).

Furthermore, Kavtaradze (2000) associates, although in more diffuse outlines, the ancestors of the three Caucasian language families with the Büyük Güllücek, the Maikop, and the Kura-Araxes cultures, respectively, all of which converged in eastern Anatolia in the 4th and early 3rd millennia BC. Large-scale movements of people westward from Anatolia into the Balkans are known to have occurred during the Early Helladic II or in Early Helladic III (i.e., 2500–2300 BCE, contemporaneous with the Kura-Araxes Culture) (Hood 1974; Diamant and Rutter 1969). To what this may be attributable, and whether it can be said to have affected eastern Anatolia and the west, are not entirely clear. But, if eastern Anatolia is indeed the place where, as Kavtaradze suggests, an amalgamation of native Anatolian and early Indo-European-speaking tribes from either the west or north came together, then periodic infiltrations into the Caucasus by speakers of various proto-Caucasian languages, which subsumed older

autochthonous populations, would be responsible for the presence of Kartvelian-, Abkhazo-Adygean-, and Nakh-Daghestan-speakers today (Figure 3).⁴

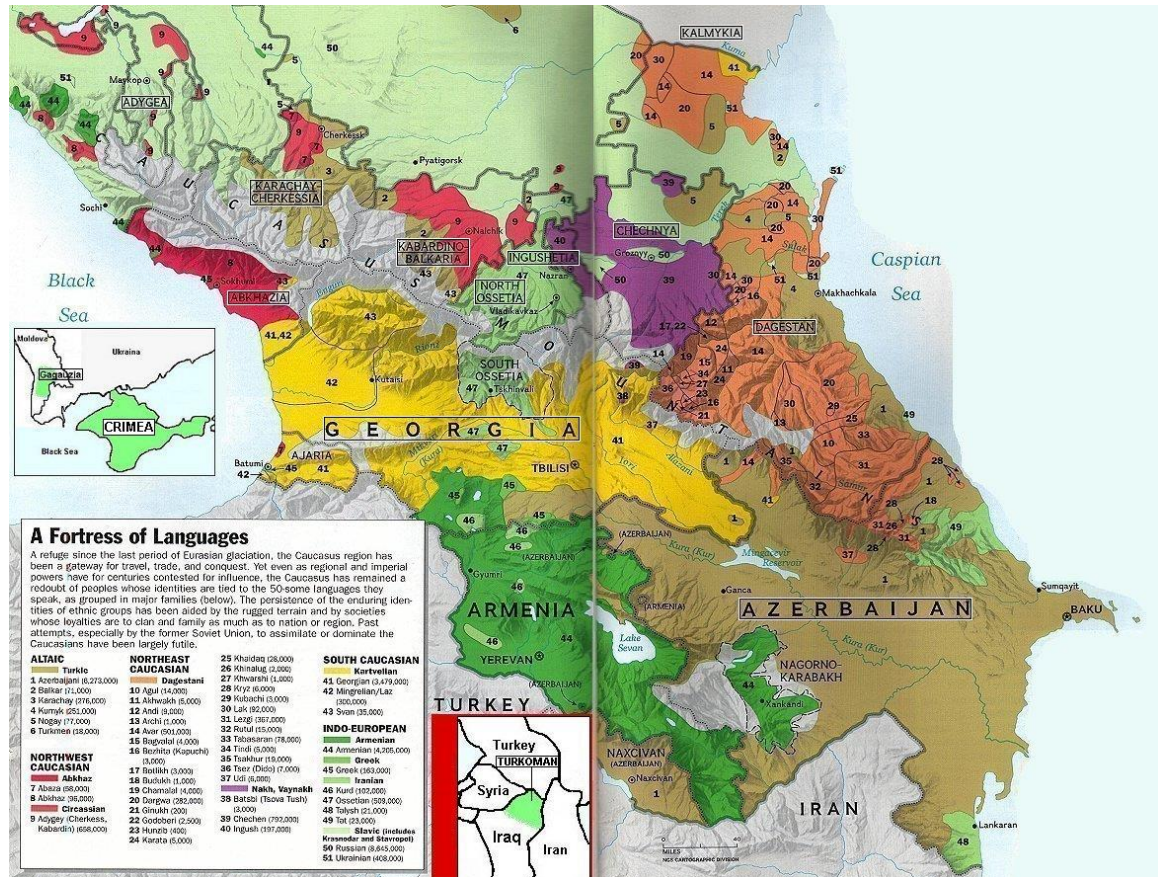


Figure 3. The geo-linguistic composition of the Caucasus (<http://imgarcade.com>)

While there is no consensus about the relationship between the Kartvelian and Northwest and Northeast Caucasian language families (which sometimes are considered

⁴ It should also be remembered that the relationship between Paleolithic, Mesolithic (Epipaleolithic), and Neolithic in Anatolia are a critical yet virtually blank spot in the narrative of ancient Near Eastern population histories. Cave sites such as Direkli (Arbuckle and Ereğ 2012) and Öküzini (Kuhn 2002) have yielded both Epipaleolithic (c. 20–11,000 BP calibrated) and Neolithic, and thus the possibility that certain lineages and linguistic features from there are very old indeed.

a macro-family) (Catford 1978; Tuite 1999), a consensus theory as to how the Kartvelian language family itself is structured has emerged (**Figure 4**). Svan's status as the oldest and most differentiated of the Kartvelian languages would suggest that it first split off first from the proto-Kartvelian speech-group, and then was spread into the sparsely populated western Georgian lowlands in the 3rd millennium BC (Chirikba 2008). This was followed by an expansion of Zan speakers (the putative ancestor of Laz-Mingrelian), who may have pushed the Svan-speakers (as well as possibly speakers of Northwest Caucasian, including Abkhaz or proto-Abkhaz) further into the highlands. This second expansion event would then have been followed by the arrival of Georgian-speakers, whose language was gradually formed through several processes, including the rise of the kings of Kartli-Iberia in the 4th to 8th centuries CE, and their adoption of Christianity (see Suny 1994: 20-23).

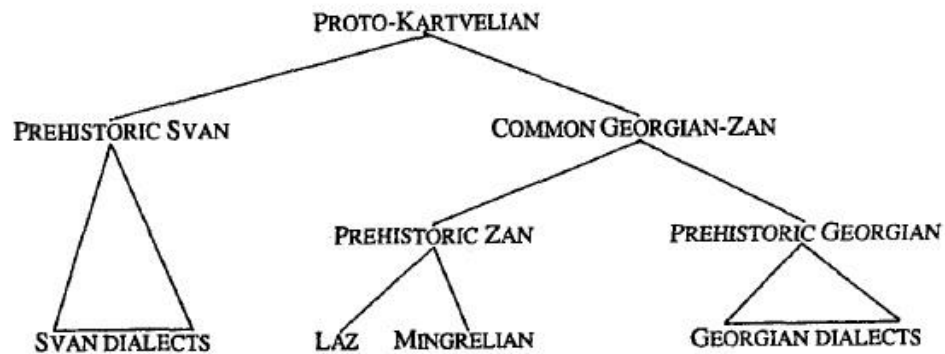


Figure 4. Kartvelian Language Family Tree (Tuite 2007)

An alternative model for linguistic genealogy (see ლომასტაძე and ობიძე 1996) depicts Svan as deriving from a common Zan-Svan substrate, thus suggesting a more recent division of these languages (**Figure 5**). However, given that this division may have occurred outside Georgia, it does not decrease the likelihood that Svan-speakers settled first in western Georgia.

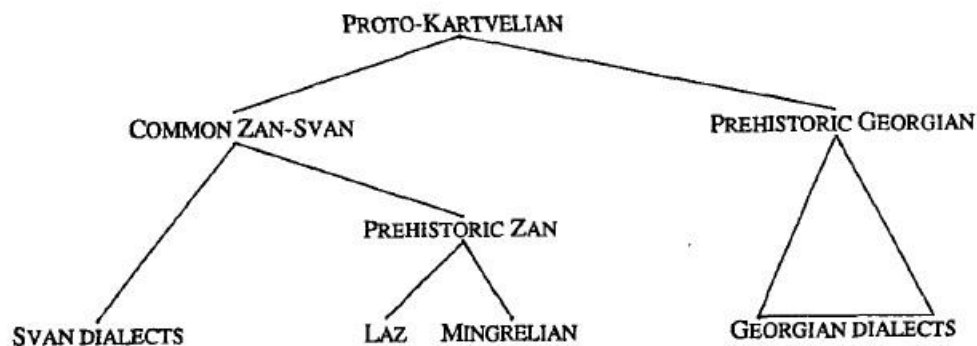


Figure 5. Kartvelian language family tree (alternative hypothesis) (Tuite 2007)

Beyond these theories, nothing is known about the linguistic affiliations of any of the inhabitants of this part of the Caucasus until the appellations of Classical authors. The clearest and earliest identification of Svans comes from Strabo’s *Geography*, written sometime around the beginning of the Common Era. He notes that: “Among the tribes which come together at Dioscurias ... are the Soanes, who are ... superior ... in power ... and hold possession of the heights of the Caucasus above Dioscurias” (Strabo XI:II: 19). The description of locality for the “Soanes” in Strabo’s *Geography* conveniently fits modern Svaneti, inasmuch as Dioscurias is modern-day Sukhumi

(capital of Abkhazia) and the heights of the Caucasus above would be eastern Abkhazia and Svaneti. If Pliny the Elder's (VI: V) claim (roughly contemporaneous to Strabo's work) that 130 interpreters were required to do business in Dioscurias is not boldly exaggerated, then it is all the more significant that Strabo chose to mention the Soanes as being among them.

Much of Books II through V of Agathias Scholasticus' *Histories* are devoted to the Byzantine-Persian conflict that took place in Lazica from 550-60 CE. There are numerous references to the Misimians in the *Histories*, a people subject to the Lazicans. As we shall see, there may be good reason to associate the Lazicans with the Svans. At this time, the Byzantine army and their Laz allies were camped in Lazica awaiting a Persian offensive under Nakhoragan. Emperor Justinian's policy was to dispense financial incentives to the peoples living north of Lazica to ensure their allegiance, as well as, presumably, the safe passage of goods to the North Caucasus.

The first recipients, geographically speaking, were the Misimians, who guarded a principal overland route through the Caucasus to the northeast of Lazica (i.e., present day Samegrelo, possibly including Zemo-Svaneti), and to the east were a people called Apsilii (identified with the Abkhaz; Hыckов 2011; see Agathias III: 15 for an observation on the linguistic and cultural odds at which these two close geographic neighbors stand). Soterichus, the senior officer in charge of doling out the money, was killed by the Misimians (III: 16). Whether this happened accidentally (III: 17), because the Misimians had already decided to defect to the Persians, or the reverse, is unknown, but as Braund notes (1994: 310), Persian diplomacy and incentive was likely no less

active than that of the Byzantines. Later, more envoys were sent to take the money back but they were also killed (IV: 15), and hostilities between the Byzantines and Misimians ensued (IV: 16-20). Subsequently, because the Persians failed to protect the Mismians as promised, the latter were forced to reconcile with the Byzantines, and return the incentive money (IV: 20).

In IV: 15, Agathias describes the arrival of the Byzantines at Tibeleos on the Misimian-Apsilian border. Although Tibeleos has yet to be identified as a city, and was possibly a fort (D. Braund, pers. comm.), and since it is possible that Abkhaz-speaking peoples were living further south along the Black Sea coast, the location of the land of the Misimians must also have been adjacent to Zemo-Svaneti, the region in which the ‘Soanes’ are located in Strabo’s *Geography*. However, we cannot be sure whether or how the Misimians and the Soanes were related, especially given the putative control of the former over the North-South Caucasus trade routes, which would have run through Svaneti. Since they are referred to separately in the historical literature, it seems they were, at the time, distinct polities.⁵

⁵ The uncertainty surrounding the linguistic affiliation of the numerous tribes and other polities present in eastern Anatolia and the South Caucasus during Antiquity will likely never be resolved. This is due not only to lack of reliable historical record, but also to the problem of overlapping nomenclature. Marr once claimed, for example, that the word ‘Svan’ must be an exonym, for it and its various historical permutations do not comply with Svan grammatical norms as they are currently understood. However, this interpretation is categorically rejected by Tuite (pers. comm. 2015) inasmuch as ‘is in fact one of the few Kartvelian ethnonyms that clearly goes back to the protolanguage, and its etymology is quite regular’. Marr, instead, linked the first syllable of ‘So-[an]’ to the Svan endonym, which is variously ‘Mushni’ or ‘Mushani’ to ‘Mushki’/‘Meskhi’, a term which has been linked in turn to Meskhetian Turks, to produce ‘Soumekhi’ (the Georgian word for Armenians) (Thomas 1957: 151, notes 2 and 3; see also Tuite 2008: 41). From this etymological work, however, very little information about Svan history and processes of ethnogenesis can be gleaned. No less satisfying an etymological observation was made by Janashia (1942) concerning the Karachay-Balkar name for Svans, which is ‘ebze’, a word Janashia links to ‘Obezi’ and thus ‘Abazgia’. According to Menander Protector (1985: 127), the Misimians were still residing in Dali (near the Kodori River and Gorge in present day Abkhazia) gorge and its vicinities in the sixth century CE. Following their defection to Persia, Byzantine soldiers allegedly slaughtered about

According to Menander Protector (6: 1), the Byzantines asserted that control over Lazica meant control over Suania. In support of this view, they produced a document showing that the Suan kings had been appointed by the kings of Lazica through at least the first half of the fifth century CE. Braund (1994: 312-14) points out that the tributary status of the Suani under Lazica, and the gifts of grain received by the Suans, may have been either simple exchange or remittances designed to stop the Suans from coming down the mountain and taking the grain anyway. Unlike the Lazicans, and for whatever reason, it seems the Suans preferred Persia to Byzantium (Menander Protector 6:1). When in 561-2 BCE, Persia ceded Lazica to Byzantium, it does not seem to have relinquished Suania.

The struggle for suzerainty over this strategic highland region and control of trade routes to the North Caucasus continued until the Arabs arrived in the 8th century CE. Their appearance occurred well before Svaneti disappears from the historical record until the 11th century CE, when the Georgian Kingdom consolidated its territory and a feudal system was established in Svaneti, with the exception of Upper Bal, where individuals remained free. During this period, nobility or local monasteries owned the land under the auspices of local churches, and serfs worked on local plots. The serfs were bought and sold as needed (Гасвиани 1980: 31, 42). This process, which continued even after 1871, at which time serfdom was outlawed (Авалиани 1913), may have in and of itself contributed to a reshuffling of age-old settlement patterns in Svaneti.

5,000 warriors and 10,000 civilians (see also Agathias II:18 – III:28). Subsequently they disappear from the historical record. Инал-ипа (1976) speculates the Misimians were, in fact, an Abkhaz-speaking tribe.

Unlike some other regions of the Caucasus (e.g., Chechnya), whose demographic histories were scrambled (and very nearly obliterated) due to Stalinist policies, Svaneti seem to have remained static during the Russian imperial and Soviet periods (Suny 1988). It was during the late 19th century that physical anthropologists and biologists first examined Svans and other Caucasus peoples in terms of population variation (e.g., Абдушелишвили 1964; Пантюхов 1893). While these works are considered classic in their way, their results are less important to us now, and will thus remain undescribed in this study.

Ic. Abkhazia and Ossetia: Their History and Ethnogenesis in Brief

Unlike Svaneti, Abkhazia and Ossetia, especially their lowland regions, have long histories of human occupation reaching back into the Lower Paleolithic. In both regions, numerous lithic points and scrapers are described in the literature, although not fully contextualized due to lack of skeletal remains (for Abkhazia see Бердзенишвили 1960; Бердзенишвили and Гзелишвили 1961; Любин 2011; Соловьев 1971; Воронов 1969; Колбутов 1961; for Ossetia, see Верещагин 1957; Liubin 1958, 1960b, 1977). The Upper Paleolithic of Abkhazia is known mainly from three sites—Ariancha (Замятнин 1937, 1961; Коркия 1998a, 1998b; Церетели et al. 1982), Okumi (Тушабрамишвили 1963), and Khupinipshava (a/k/a Kholodnyy Grotto) (Соловьев 1973)—where a variety of tools (knives, awls, needles, and some harpoon-like fishing implements) were found. The same culture is thought to have extended north at least as far as Sochi and south into Colchis (ცერეტელი 1973). The only obtainable

established age for these sites comes from Akhshtir Cave in the Sochi region, which is dated to $19,500 \pm 500$ BP (Чердынцев et al. 1965; Паничкина and Великова 1962).

Although as yet undated via radiocarbon (or dated but unpublished), the Apiancha cave site features cultural layers belonging, like Darkveti to the south, to the Upper Paleolithic, Mesolithic, and Neolithic periods (Паничкина and Великова 1962). As with Darkveti (see below), the question remains as to whether continuous occupation means habitation by continuous lineages (the same people). It is the opinion of some researchers (e.g., ჯაფარიძე 1991-2) that the Mesolithic culture in the eastern and northeastern Black Sea region, as typified by Apiancha and similar sites, is a formal continuation of Upper Paleolithic, especially with regards to the microlithic tool industries. The Neolithic transition in this broad region is a more complex matter. However, there is still supposition, based on the evolution of these same industries, that typological continuity may be recognized in the archaeological data (ბუბოჯიძე 1972; Церетели 1974) although the excavations undoubtedly began in the prior decades.

In South Ossetia, Acheulian and Mousterian sites are well described (see Любин 1958, 1959, 1960b) and several sites feature long-term habitation, such as Kudaro (Верещагин 1957; Любин 1959). However, Paleolithic sites in South Ossetia are thus far rare. Those that have been found are described in Liubin (1960b, 1977) and Hijirati (2003). Unfortunately, these researchers have made little attempt to schematize lithic typologies or population continuity in this region, or to determine if and how the industries and settlement patterns in these two proximate regions are related. Accordingly, there is very little that we can surmise about the peoples living in these

regions during the Upper Paleolithic and Epipaleolithic. Yet, it is important to realize that there is no evidence for any major population event along the shores of the northeast Black Sea, and in the lowlands and gorges or western Georgia, that would interrupt the continuity of lineages between the Upper Paleolithic and today. Even if, as Kavtaradze (2000) and others suggest, the Caucasian peoples and their languages descend in the greater part from the ancient peoples of Anatolia, it cannot be assumed that a complete break in population continuity occurred with their arrival and settlement.

The ethnogenesis of Abkhazians is a matter with even less scholarly consensus than that of the Svans. Unlike the Svans, Abkhazians are not mentioned by name as part of the highly complex cosmopolitan picture of Dioscurias portrayed by Strabo and Pliny the Elder (see above), nor are they mentioned in Arrian (1976-83). Various philological readings of geography and topography have yielded theories about Abkhaz ancestry (e.g., Chirikba 1991; Map 1938), and which tribes may have contributed to the ethnogenesis, although such treatments, especially those published since the Georgian-Abkhaz War of 1992-93 (e.g., Gamakharia et al. 2011) are tendentious at best. We are on firmer ground with the mention of Abkhaz people in the diaries of the Dominican monk and Archbishop of Sultaniya (also first bishop of Nakhchivan), Johannes de Galonifontibus, dated 1404 CE, which state that, “[b]eyond [the Circassians] is Abkhazia, a small hilly country ... They have their own language ... To the east of them, in the direction of Georgia, lies the country called Mingrelia” (Tardy 1978: 93-94).

Because it is difficult to ascertain the exact geographic position at the time of his observations, “beyond the Circassians” is difficult to interpret. If Mingrelia is considered to lay to the east, or southeast, then we are more assured in positioning the Abkhaz people in the same place they currently dwell. We are further assisted in this regard by another travel writer of the seventeenth century CE, Evliya Çelebi, a half-Abkhazian citizen of Ottoman Turkey who spent his most of life travelling and recording anthropological and linguistic details of the peoples he encountered (Dankoff 2006). He eventually made his way up the western Black Sea coast and visited the Abkhaz, and his reckoning of the Mingrelians confirms that of de Galonifontibus (Tardy 1978).

Ossetia is a different matter. Its primary language, Ossetian, belongs to the Eastern Persian subfamily of Indo-European, and its people attribute their ethnogenesis to the arrival of the Alans, a confederation of semi-nomadic Sarmatian tribes whose pan-Eurasian migrations are well attested (see Alemany 2000). However, the Alan-Ossetian connection suffers from a kind of double scholarly bind. While there is neither a strong indigenous nor strong critical assessment of this relationship, we also cannot be sure of the extent to which Klaproth (1822), the European traveler chiefly responsible for the theory, influenced the indigenous tradition and/or vice versa (see below for more on this point). Furthermore, we can by no means be certain that the presence of an Indo-European language in the South Caucasus, one very likely, in fact, descended from the language of the Alans and/or other Indo-Persian-speaking steppe nomads, means that the modern day speakers are biological descendants of such populations.

1d. Objectives of the Dissertation

Given the complex ethnographic and historical background of the region, we analyzed Svan mitochondrial DNA (mtDNA) and Y-chromosome variation to elucidate their genetic history. Our main objective was to document human biological diversity in Svaneti. In order to do this, we characterized mtDNA and Y-chromosome variation in Svan participants to determine their maternal and paternal haplotypes. Several recent studies utilizing these genetic markers (Balanovsky et al. 2011; Bulayeva et al. 2003a, 2003b, 2004) have demonstrated extremely high paternal genetic diversity in Daghestan populations.⁶ If similarly high levels of genetic diversity (i.e., low haplogroup diversity but high haplotype diversity) coupled with novel genetic lineages are found in Svaneti, then we might propose that Svan populations originated from Neolithic settlement events (as Balanovsky et al. did) or even earlier. If, on the other hand, their genetic diversity is found to be low (i.e., low haplotype diversity and/or lack of shared ancestry with neighboring groups), then we might hypothesize that more recent settlement events (i.e., post-Neolithic) also occurred there, perhaps with the emergence of Kartvelian languages in the region.

There is continued debate about the influence of Neolithic and post-Neolithic expansions on Caucasus populations. The presence of specific genetic lineages associated with Neolithic and post-Neolithic-era expansions (e.g., Y-chromosome haplogroup J and mtDNA haplogroup T) suggests some movement into the region

⁶ This research involved the analysis of microsatellites or short tandem repeat (STR) loci, as well as genomic markers related to two complex clinical phenotypes (i.e., mental retardation and schizophrenia).

during this period, both from the south (Middle East) and the southwest (Anatolia) (Battaglia et al. 2009; Cinnioglu et al. 2004; Nasidze et al. 2004; Weale et al. 2001). However, Kartvelian languages are usually thought to have made their appearance in the region no earlier than 2000 BCE (Klimov 1994). Since most studies of genetic variation in the region indicate that the majority of lineages present there are more deeply rooted, it would appear that multiple peopling events occurred in the Caucasus. These may well not have been events per se, but rather gradual influx of settlers from different regions, whose otherwise nomadic presence was given permanence during the Neolithic. We will therefore also assess, through analysis of specific maternal and paternal lineages, the possible deeper connections between Caucasus and other Eurasian populations in prehistory.

Our second objective was to compare the genetic diversity of Svaneti with that of its western and eastern neighbors, Abkhazia and South Ossetia, respectively. By focusing on the extent to which Svans share lineages, and thus common ancestry, with proximate non-Kartvelian-speaking populations in the Georgian highlands (or more precisely, within its purview of breakaway regions), we can glean insights into the histories of these populations. If the Svans, Abkhaz and Ossetes share a common genetic ancestry, then this fact may contribute to an enhanced understanding of the peopling of the Caucasus.

Our third objective was to examine whether Svan genetic variation is structured by regional residence within Svaneti, which could potentially explain patterns of regional settlement. Should phylogeographic patterns of haplogroup distribution in

Svaneti emerge, these could potentially be explained in several different ways. First, if there are haplogroup or haplotype frequency distinctions between Upper and Lower Svaneti, then this might indicate the occurrence of separate gene flow events, from the North Caucasus, the Levant or Anatolia, or perhaps elsewhere in the greater Near East. Second, topographic variation can encourage and restrict gene flow (e.g., Tarkhnishvili et al. 2015), but in Svaneti, a potential ‘refuge area’, the case would more likely be restriction. Third, genetic drift may have changed gene frequencies over time. Since we know that in contemporary Georgia, Svan men sometimes marry lowland women, but rarely the converse (Topchishvili 2005), genetic drift due to such social practices may be responsible for the maternal gene frequencies we observe. If high percentages of mtDNA haplogroups H and U1, and/or Y-chromosome G, I, and R1a are observed, especially in Upper Svaneti, then we might conclude that there has been genetic exchange between Svans and populations from Karachay-Circassia (to the immediate north) and perhaps also the Pontic region, given the high frequencies of these lineages in those regions (Yunusbayev et al. 2012). Should Svans show higher frequencies of lineages such as Y-chromosome haplogroups J1, J2, E1b1b, G2a, or R1b, or mtDNA haplogroups HV or T, we might conclude that Svaneti has been genetically influenced by Near Eastern populations, in which these lineages commonly occur (Derenko et al. 2012; Fernández et al. 2014; Lacan et al. 2011; Nasidze et al. 2005). Moreover, if unique haplotypes or deep-rooted clades are detected in Svaneti, then this could possibly indicate very long term habitation (perhaps since the Upper Paleolithic), as has been seen in geographically similar regions of Daghestan, where this pattern is

correlated with the distribution of mutually unintelligible languages (Bulayeva et al. 2003a, 2003b, 2004; Balanovsky et al. 2011).

Further, it is highly likely that any age-old settlement patterns were shuffled by the sale and movement of serfs in the early modern period. Thus, this dissertation will also take note of the historical processes which may have influenced patterns of genetic diversity in Svaneti, such as those rooted in commercial activity or even imperial or post-imperial demographic reordering (see Braund 1994; Moushegian et al. 2000; Naimark 2010; Suny 1994). Although very little may be said about the movements of individual serf families between Upper and Lower Bal, this fact alone is worth pointing out. Similarly, while Georgia in general, and Svaneti in particular, were largely immune to the demographic re-ordering (not to mention ethnic cleansing) that affected their neighbors to the north (e.g., Chechens and Circassians) (Moushegian et al. 2000; Naimark 2010; Suny 1994), there is some possibility that refugees from these regions ended up there.

Overall, this dissertation will describe the population history of Svans by placing them into Caucasian and Near Eastern (West Asian) genetic contexts. It uses a phylogeographic approach to dissect the historical layers of Caucasian peoples, about whom the Georgian historian Giorgi Melikishvili asserted “have been settled in the territory of Transcaucasia and the North Caucasus from the most ancient times” (Меликишвили 1959). It what follows, Section II reviews the peopling processes of the Caucasus, as they can be gleaned from the archaeological, linguistic, and genetic literatures.

CHAPTER II: PREHISTORY OF THE CAUCASUS

The Caucasus is often called the bridge between worlds, inasmuch as it serves as a connection between the southern world of the Middle East, Anatolia, Mediterranean, and Africa, and the northern world of the Russian steppes and East Asia. As bridges go, it is a rather difficult one to cross, given that the snowcapped mountain peaks and deep gorges block easy transit from one region to another. Nevertheless, the highlands and valleys of the Caucasus are home to some 30 million individuals who speak sixty different languages belonging to five different language families⁷ and as many overlapping tribal and ethnic groups, which represent not only the three Judeo-Christian religions but also some pre-Advent belief systems. Thus, this comparatively small region is one of the most socially diverse places on earth. Moreover, numerous studies have revealed considerable genetic diversity in Caucasus populations, which in turn indicates a high degree of genetic differentiation between them.

How did such a small region, an area slightly larger than California, come to be so culturally and biologically diverse? What forces of geography, political formation, biology, and ancient and modern history shaped the populations of the Caucasus? And from whence did its myriad cultural traditions arise?

This chapter will present the case for a four-phase pattern of population settlement and interaction in the Caucasus. The process begins with the ancient settlement of regions with various Upper Paleolithic and Epipaleolithic sites, when

⁷ Notwithstanding continued disagreements on classification of Caucasian as one, two, or three families; this study presumes three, Northeast (or East) Caucasian, Northwest (or West) Caucasian, and South Caucasian (or Kartvelian) (Nichols 2003; Schulze 2009; Tuite 2008).

some of the raw materials for Caucasus populations were established. It continues with complex cultural transitions in the Neolithic, with concomitant changes in settlement patterns and food production in an as yet limited number of known permanent settlements. With the beginnings and refinement of metal production, there came many new technological horizons apparently related to others in the greater Near East and southern Russian steppe. Finally, a profound demographic transition and consolidation of identities occurred during Antiquity and in the era of modern empires. Unlike continental Europe and the Middle East, which are more ‘cosmopolitan’ in their patterns of genetic variation, the topography of the Caucasus has allowed for a great deal of entrenchment in certain areas, at least by males, a fact which permits some degree of inference into the length of habitation and timing of settlement (e.g., Balanovsky et al. 2011).

IIa. The Caucasus as a Geographic Entity

A geographic definition of the Caucasus, like all regions formed partly by geography and partly by history, tends to be elastic. Does it belong Europe or Asia or both? Do Rostov Oblast, Kalmykia, and eastern Turkey belong to it? What about the Lenkoran Lowlands and Talysh Mountains of Azerbaijan? These questions are important because the borders and frontiers of the Caucasus determine which populations are relevant to a study of Caucasus populations. Thus, for example, ethnic Azerbaijanis live both in Azerbaijan proper and also in Iran, due to historical

contingencies, yet this doesn't make them different peoples culturally and genetically speaking.

It is for this reason we will define the Caucasus not by the trajectory of the mountain range itself, as its foothills and lowland steppes would also include areas of northeastern Turkey and northwestern Iran, but rather by its political delimitations.⁸ All together, the Caucasus region, as we have defined it, encompasses approximately 441,800 km² including the disputed territories. Its total population, based on a tally of a number of censuses, is approximately 30,800,000, inclusive of all areas north and south.⁹ The area is named for its defining geographic feature—the Caucasus Mountains—which are part of an alpine and glacier system running east-west between the Black and Caspian Seas that divides the Caucasus area into two socio-political halves, northern and southern.¹⁰

⁸ The southern border of the South Caucasus, also the southern border of the former Soviet Union, runs partly along the Arax River, with a further portion of Azerbaijan below this, as determined by the 1828 Treaty of Turkmenchay between the Persian and Russian Empires (see Atkin 1980: 158-61; Entner 1965: 6-7, 10-11). The western border, with Turkey, is the result of the 1921 Treaty of Kars, in which the Bolsheviks ceded Kars to the Turks in exchange for Batumi (Karabekir 1988: 855-59, 884-93). The remainder of the western border is demarcated by the Black Sea, and the eastern border is the Caspian Sea. The South Caucasus, also called the Transcaucasus, includes the sovereign nations of Georgia, Armenia and Azerbaijan, as well as three *de facto* independent states, including Nagorno-Karabakh (an actively disputed enclave surrounded by Azerbaijan), and South Ossetia and Abkhazia (two breakaway regions from Georgia, both with land borders against the Russian Federation). The total area of the South Caucasus is 186,000 km² and the total population of these states is approximately 16,730,000, inclusive of three breakaway regions.

⁹ These totals are our own calculations based on data from the Federal State Statistics Service [of Russia] (Федеральная служба государственной статистики). It has been quite some time since proper censuses were undertaken in Georgia.

¹⁰ The mountain system itself is divided into two distinct parallel ranges, the Greater and the Lesser Caucasus. The Greater extends about 1200 km southeast from the Krasnodar port of Sochi, on the northeastern shore of the Black Sea, to the lowland area north of the Caspian Sea port of Baku. The Lesser runs parallel to the Greater at a distance of about 100 km to the south, and includes the Trialeti and Javakheti ranges of southern Georgia, and Mount Aragats in Armenia (Думитрашко 1966: 21-24). The Greater and Lesser Caucasus ranges are connected by the north-south Likhi Range, which separates the Kolkhida Lowland from the Kura-Aras Basin, and thus divides Georgia into two geographic areas,

Formally, the Caucasus is a pair of cul-de-sacs, with some amount of accessibility head to head. Numerous footpaths connect Georgia with the North Caucasus, but their ways are tortuous and seasonally dependent (Левин 1938). Even if the North and South Caucasus were never fully cut off from each other, the question of how and when to consider them separately is very important because certain cultural traits permeate the mountain range and others do not (Catford 1977: 284-5; Yunusbayev et al. 2012). Since there is more geographic obstruction within the Caucasus than between it and its neighboring regions, studies of population history and phylogeography¹¹ must therefore look primarily outward to the frontier areas to the north, south, and southwest of the region, including the Black Sea as a special case of frontier zone, and secondarily at population movements between the regions. This

historically known as Colchis and Iberia (ბერძენიშვილი 1990: 560-62). The Lesser Caucasus and the Armenian Highland, to the south, constitute what is known as the Transcaucasian Highland (Allen 1942: 226-27; Гулиашвили 1964: 17). Although some researchers and news agencies consider the entire Caucasus region to be part of Europe, the geographer's divide of Europe from Asia runs, strictly speaking, east to west along the Great Caucasus Watershed, as suggested by mountaineer Douglas Freshfield (1869: 71; see also Moores and Fairbridge 1997: 34; ყუციევ 2005: 52-61; von Haxthausen 1854). Therefore, however arbitrary it may seem, the Russian federated states that make up the North Caucasus (e.g., Daghestan, Chechnya) are considered to be part of Europe, and the sovereign nations of the South Caucasus (Armenia, Azerbaijan, Georgia) part of Asia. It is remarkable that the Caucasus was never fully and permanently subsumed by the greater geographical rubrics of Middle East and Russia, in spite of great imperial effort. This says something important about geography of the region, but also about the defenders of it. Any explanation of cultural and genetic diversity in the Caucasus, as well as the interest and challenges invading empires have encountered in their efforts to subdue the indigenous peoples, must begin with the difficulty and openness of the terrain, as well as its varieties.

¹¹ Although phylogeography has population biology beyond the scope of this study, for our purposes it is the method of accounting for the geographic distributions of human individuals due to historical processes (e.g., migration, settlement patterns).

simple fact goes a long way in explaining patterns of regional variation as they pertain to languages, ethnic identity, and genetics.¹²

Given its range of altitudes and position between two seas, the Caucasus features extremely diverse environments, ranging from perennial glaciers and craggy mountain valleys to arid platte land to subalpine meadows and dark coniferous forests (**Figure 6**). Lush subtropical valleys and deciduous forests found along the coast of western Georgia (Zimina 1978: 481-83). Prior to intensive agriculture, much of this region was covered with mixed broad-leaf forests and swamp trees stretching from the Colchis lowland to Sukhumi (Квавадзе and Рухадзе 1989). Oak and juniper forests likely covered much of southern Georgia, and probably northern Armenia until relatively recently (Connor et al. 2004: 230-31).



Figure 6. Caucasus glaciers (contemporary view)
(<http://earthobservatory.nasa.gov/Features/Kolka/>)

¹² Genetic studies showing diversification of non-human mammal species in the North and South Caucasus also support the idea that the Caucasus has long represented a semi- or at times impermeable biogeographic barrier (Manceau et al. 1999; Orth et al. 1996; Seddon et al. 2002).

There are many schemes for dividing the region topographically and ecologically. Based on his study of Digor artifacts from North Ossetia, Motzenbäcker (1996: 13-20) proposed five basic geographic zones into which the Caucasus region may be divided. These include (1) the North Caucasian plain, bounded by the Kima and Manych Rivers; (2) the Great Caucasus mountains themselves; (3) the South Caucasian river basins and tributaries, flowing mainly through Georgia and Azerbaijan; (4) the Lesser Caucasus; and (5) the volcanic Armenian highlands, which give way to Anatolia to the west.

Such variant and abundant conditions in the lowlands, well known to evolutionary biologists as a refuge area for mammals (Eronen and Rook 2004: 336; Vekua and Lordkipanidze 2008), must also have been very appealing to both early hominins and later *Homo sapiens* who roamed the gallery forests and open plains in search of fruit and game. The fossil ape *Udabnopithecus garedziensis* (also known as *Dryopithecus garedzianus*) also lived in the Udabno region of southeastern Georgia during the Upper Sarmatian or Lower Meotic (8 – 8.5 mya). The presence of this hominoid allows us to consider the Caucasus an important corridor for Miocene (and continuing) faunal movement (Бурчак-Абрамович and Габашвили 1945; Gabunia et al. 2001). Moreover, given the possible links with other *Dryopithecus* of Eastern Europe, these data indicate connections between the Mediterranean and Asia via the South Caucasus (Maschenko 2005).

Late Pleistocene glaciers covered the North Caucasus region, and parts of the South in an apparently uneven pattern (Gobejishvili et al. 2004: 130-33). Lacking

extensive data from pollen cores and oxygen isotopes, the timing of the glacial maximum in the Caucasus is still debated, with estimates in the literature ranging from >44 KYA to the interval 14-10 KYA (Gobejishvili et al. 2004, Щербакoва 1973, Варданянц 1937). Golovanova and Doronichev (2003) have extrapolated a chronology for climatic shifts in the Caucasus (**Appendix 1**). Following the Interpleniglacial Period, Golovanova et al. (2012) estimate the duration of the last glacial maximum (LGM) to have been 25-18 KYA, after which a new Epipaleolithic industry appeared between western Georgia and the southwestern Russian plains. According to Bondarev et al. (1996), most deglaciation had occurred by c. 10,000 BP, after which smaller valley glacier advances continued for a time. For this reason, human occupation during the Upper Paleolithic and Epipaleolithic may have been intermittent and temporary, as it was across the Caspian in the Southern Aral region (Boroffka 2010: 283).

Whether the glaciers caused a total interruption in population continuity at any time in the Caucasus, or if pockets of humans remained isolated within gorges and valleys throughout the cold times, remain open questions. Passages over the Caucasus range during this time were surely few and difficult. However, along the western shores of the Caspian, the evidence of Mousterian tool culture settlements (Амирханов 1986a: 1-7) indicates that human passage was possible during the Lower Paleolithic, as well.

The physical extents of Pleistocene and Holocene glaciations in the South Caucasus are still a matter of some uncertainty, although this is not due to lack of initiative. For decades, the Penck and Brückner (1901-9) mechanical model, based on work in the Alps, was authoritative. More recent geomorphological research (e.g.,

Маруашвили 1956; Щербакова 1973) has suggested the Late Pleistocene glaciers were smaller and more of the valley-type (Bondarev et al. 1996; Solomina 2012). According to research by Gobejishvili et al. (2004), the central and western Caucasus Mountains have a glacial character that is different from that of the eastern Caucasus and Caucasus Minor. In western Georgia and Abkhazia, lower rock thresholds of Pleistocene glaciers are found at 1900-2000 meters, although some corrie-type glaciers reached down as far as 1600-1700 meters. The lowest known altitude at which a glacier tongue terminated is the Nenskra Glacier in Svaneti at 600-680 meters. Large valley-type glaciers formed in numerous river valleys and basins such as the Chkhalta, in which only three descended to the valley floor.

Given that many areas of the Black Sea Coast and inner Georgia stand well below the 1600-meter line, there is the potential for long-term refugia in both the North and South Caucasus lowlands, and thus for the continuity of human populations into the times of Neolithic and later settlement events. Given the altitude, there was also the potential for human settlement in the highland areas throughout the colder periods. For example, a combined pollen analysis and radiocarbon study of organic deposits in the Dziguta River, located southeast of Sukhumi, indicate a correlation between the LGM in the region and a proliferation of Upper Paleolithic industries (Arslanov et al. 2007). However, these sites were only recorded along the western Caucasus mountain ridges facing the Black Sea and on the northern Caucasus slopes, and nowhere in the inner areas of the Lesser Caucasus. Such observations suggest that either these areas were less suitable for human settlement at the time (Arslanov et al. 2007: 126) or simply that

settlements there have yet to be identified or defined. Whether or not Würmian glaciation reached all of the lowland and even highland valley areas of Armenia and Azerbaijan is an important but poorly researched question, inasmuch as even small pockets of Upper Paleolithic or Epipaleolithic populations surviving through the LGM, absorbed by post-glacial or Neolithic populations could have affected the gene pool of the Caucasus.

In the North Caucasus, the picture is apparently even more complex and wanting of further research. It has been theorized that the Manych-Kerch Spillway, an extinct body of water which connected the Caspian Sea basin to that of the Sea of Azov by means of a natural run-off (**Figure 7**), reached its highest peak of activity during the Khvalynian transgression, c. 13.5 – 12 KYA, which was coeval with the various Late Glacial episodes and ice sheet recessions in the higher latitudes (Dolukhanov et al. 2009). Until the disappearance of this obstacle following the maximum of the Upper Khvalynian transgression, c. 12.5 – 12 KYA, the region bounded by the spillway, the two seas, and the northern foothills of the Caucasus Major must have existed as a kind of island, into which, evidently, Upper Paleolithic technology and anatomically modern humans did not penetrate.



Figure 7. The Manych-Kerch Spillway (http://paleogeo.org/manych_en.html)
(Key: Кавказские Горы=Caucasus Mountains; Маньч-Керченский Проллив=Manych-Kerch Spillway)

The boundedness of the environments within this region also favored a prolongation of Mousterian techniques. Layer 2 (<10,000 YBP) at Mezmaiskaya Cave, for example, has yielded both Mousterian and Late Upper Paleolithic tools (Baryshnikov and Hoffecker 1994: 6-8). Given this extremely late date for Mousterian technologies, we are faced with the questions of whether this bounded region also conserved Neandertal populations, and to what extent it became a point of contact for anatomically modern humans and Neanderthals, and therefore what cultural and biological traits, if any, resulted from such interaction. Furthermore, it remains to be determine to what extent the South and North Caucasus, respectively, can be considered ‘refuge’ areas, i.e., areas off major arterial routes, into which diverse small communities

collect (i.e., take refuge from larger ones), and within which certain features come to be shared.

I**b.** The Archaeological Record of the Caucasus

I**b.**1. The Caucasian Paleolithic

Whether we consider the Caucasus region to be an ancient transit corridor, however narrow its aperture, or an outright cul-de-sac, the environmental context for human occupation in its earliest days was hospitable. This issue has been studied at length with faunal and paleobotanical evidence from various archeological sites, which indicates that hominin occupation of the South Caucasus took place in a mosaic environment of open steppe and gallery forests (Gabunia et al. 2000: 785).

Furthermore, the remains of Middle Pliocene mammals with African relatives at Kvavebi, a site in Georgia dated to about 2.5 mya, have been used to suggest the concomitant presence of australopithecines in the grasslands of western Asia, given the Saharan-Arabian desert barriers did not yet exist (Adamia et al. 2002; Agustí et al. 2009; Chumakov et al. 1992).

Even if the first hominin dispersals from the African continent did not occur prior to the Pliocene-Pleistocene transition (3.0 – 3.5 mya), it seems likely that hominins were able to reach the Caucasus via the Levantine corridor, perhaps in pursuit of game. Early Pleistocene dispersals into Western Asia and beyond are thought to have been sporadic and not to have begun before the Olduvai chron, around 1.7 – 1.5 MYA (Klein 1989, 1999; Bar-Yosef 1989, 1998; Swisher et al. 1994; Gabunia and

Vekua 1995). These dispersals were highly episodic, and evidently not all were successful (Bar-Yosef and Belfer-Cohen 2001). In fact, continuous occupation of Southwest Asia did not occur until the arrival of Acheulian toolmakers, i.e., *Homo erectus* sensu stricto (Bar-Yosef and Belmaker 2010).

The first traces of hominin occupation in the region begin at Dmanisi with the cranial remains once known as *H. georgicus*¹³ and the implements found in association with it (Rightmire et al. 2005; Lordkipanidze et al. 2007; Garcia et al. 2010; Mgeladze et al. 2010).¹⁴ Early migrants following game or other pursuits from the Near East faced formidable geographic barriers on either side of the Caspian. To the east, the deserts and semi-deserts of Central Asia stretch from Khorasan to the steppes of Kazakhstan—a huge expanse with very little useable water or other provisions, even along the Caspian coast (Макош 1982: 32-36). To the west, the Caucasus range itself presented another kind of barrier to human traffic, one traversable in pre-modern times only via a few obscure passes, most notably the western Caspian littoral. This was a route known to Herodotus (1954: 123) and Alexander (Cummings 1940: 256), and also

¹³ Initially, researchers initially classified this hominid as a separate species (*H. georgicus*), considering it to represent some kind of transitional stage between *H. habilis* and *H. erectus* but now classify it within *H. erectus* as *H. erectus georgicus* (Lordkipanidze et al. 2002, 2005, 2007; Rightmire et al. 2006; Vekua et al. 2002; Vekua and Lordkipanidze 2008).

¹⁴ Given the first early and pre-human ventures out of Africa were sporadic and rarely successful in the longue durée (see e.g., Klein, 1999), it is not possible to make any claims about continuous human occupation of the Caucasus from these earliest of times. Nor can we make any similar inferences from the presence of *H. erectus* (Gabunia and Vekua 1995), whether from the presence of a core-chopper industry also at Dmanisi (Dzaparidze et al. 1989; Bar-Yosef 1998: 235; Ljubin and Bosinski 1995), various Mousterian assemblages (see Baryshnikov and Hoffecker 1994; Hoffecker and Cleghorn 2000; Lubin et al. 2002), the intriguing Lower Paleolithic find from Stravopol described in Любин 1959, or the distribution of early Acheulean assemblages all around the region (Ljubin and Bosinski 1995). Thus, whether or not parts of the Caucasus region have been continuously inhabited since the Lower Paleolithic is still an open question.

to Mousterian toolmakers, who established several camps along the Manas-Ozen River in Daghestan, not far from its mouth at the Caspian (Амирханов 1986а: 1-7).

The Lower Paleolithic site of Kurtan, situated on the Lori Plateau of Armenia, has yielded some two hundred Early-Middle Acheulian lithic artifacts, several of which bear typological resemblance to objects from Southern Levantine sites, as well as Latamne in Syria (Belmaker et al. 2012; Doronichev and Golovanova 2010). Based on sediments and ash layers, as well as faunal remains, Kurtan is dated to c. 1.4 – 0.8 MYA. The importance of this evidence lies in the potential for a corridor between the Levant and the South Caucasus at this early date, and the potential for the development of local long-term refugia (Belmaker et al. 2012: 46) and perhaps other habitation areas. The dating for Kurtan coincides with a warming phase and concomitant expansion of habitat varieties and resources in southern Armenia, as determined through pollen core and macroflora studies (Bruch 2012).

Elsewhere in the Caucasus, there is little of which to take note until the appearance of early and late Acheulean tool assemblages in the Levant, with diminishing but nonetheless relational abundance in the Caucasian region and central Anatolia (see Lioubine 2002; Ljubin and Bosinski 1993, 1995). The majority of these are surface finds¹⁵, but a few come from cave sites.¹⁶ In spite of evidence from at least

¹⁵ Satani-Dar (Паничкина 1950), Dashtadem-3 (Kolpakov 2009), and Dzhraberd in Armenia (Любин 1961, 1981, 1984); Yastuch in Abkhazia (Коробков 1967, 1971); Chikiani, near Paravani in southern Georgia, which featured obsidian cores (Кикодзе 1986); Persati, also in southern Georgia (Ljubin and Bosinski 1993: 209); several in western South Ossetia (Lase-Balta, Kaleti, Chdileti and others in the foothills, Sona in the mountains). These Ossetian finds are key because they occur along the Liakhvi River and the Suramsk Pass—one of the few links between the South and North Caucasus (Любин 1960 and 1981; Кикодзе 1986). A few scattered Acheulean sites are reported in the North Caucasus, as well, even as far as the Psekups River (see Величко et al. 1969; Замятнин 1961а, 1961b). In Daghestan, the

200 Middle and Upper Paleolithic sites and surface find areas in the Caucasus, these periods in this region are less well understood as they are in Western Europe and the Levant.

Various cultural zone schemes have been devised to characterize the Caucasian Middle Paleolithic and the formal affinities of its technologies with neighboring regions (Beliaeva and Lioubine 1998; Doronichev 1993; Любин 1977, 1984, 1989; Ниорадзе 1992; Тушабрамишвили 1978, 1984; Тушабрамишвили and Векуа 1982; see Adler and Tushabramishvili 2004 for a full review). Most of them have focused on the South Caucasus. Although many of these studies of cultural variants neglect the importance of diachronic change and raw material availability, they are significant in formal terms.

Doronichev (1993) has proposed a tripartite system of cultural variation in the Caucasus. It includes (1) a North Caucasus variant of the Eastern Micoquian, an assemblage otherwise known in the eastern European steppe and parts of north-central Europe, and as far east as the Volga Basin (Kulakovskaya et al. 1992); (2) a

site of Darvagchai I yielded over a thousand small stone tools that have been provisionally assigned to the Lower Paleolithic (Derevianko 2006; Derevianko et al. 2006). Derevianko et al. (2007) also report similar finds at nearby Rubas-1, a Middle Paleolithic site 40km southwest of Darvagchai.

¹⁶ These include Azokh in Nagorno-Karabakh (Fernández-Jalvo et al. 2010), notable for featuring at least six occupation layers in as many caves; Gazma Cave in Nakhichevan (Zeinalov et al. 2010); Mусhtulagty Lagat (Weasel Cave), in North Ossetia (Hidjrati et al. 2003); Akhshtyr, in southern Krasnodar (Великова 1973); Treugolnaya, in Karachay-Cherkessia (Blackwell et al. 2005; Molodkov 2001); and Tsona and Kudaro I and III in western South Ossetia, again near the Suramsk Pass (see Lioubine 2000 and 2002, as well as Liubin and Bosinski 1995 for surveys). Of this set, Azokh is the most significant, not least because it has yielded the easternmost representative of *H. heidelbergensis*, but mainly for featuring an occupational period spanning the Paleolithic and the Epipaleolithic periods of the Caucasus. Любин (1989) lists several open air sites and more than forty Middle Paleolithic cave sites, fewer than ten of which are in the North Caucasus. Bar-Yosef and Bellmaker (2010: 15) stress the geographic continuity of Acheulean core-flake assemblages from the Levant to the Caucasus and Anatolia, and note the absence of such on the Iranian Plateau (see also Biglari and Shidrag 2006). However, whether the Levant and Caucasus/Anatolia continuum constitutes a settlement trajectory is not yet resolved. For all we know about these Lower Paleolithic sites, including Azokh, they may have been seasonal or sporadic hunting camps whose inhabitants made no contribution to the present-day populations of the region.

distinctively local set of assemblages in the South Caucasus lowlands which otherwise resembles Levantine or Karain (Anatolian) Mousterian finds (Otte et al. 1995a; Shea 1999, 2001); and (3) a far southern assemblage closely resembling that observed in the Zagros Mousterian (Dibble 1984; Liagre et al. 2006). These three trajectories presage, in essence, three of the four stages of human movement this dissertation proposes, and suggests these corridors of travel have always been open and active.

Mezmaiskaya Cave, a Middle Paleolithic site (40,000-35,000 BP)¹⁷ located about 50 km south of Maikop, in the Republic of Adygea, is one of the North Caucasus sites (Hidjrati et al. 2003; Hoffecker and Cleghorn 2000; Lioubine 2002; see Faerman et al. 1994 for the supposed Neanderthal infant found at Barakai Cave in Krasnodar), along with some additional sites in the South (see Джафаров 1983; Ерицяи 1975; Ерицяи and Семенов 1971; Liagre et al. 2006) that have yielded Mousterian assemblages, evidently manufactured by Neanderthal hunter-gatherers. In another area dating to the Middle Paleolithic, in the Gubs Basin of Krasnodar, researchers have noted a distinctive Neanderthal technological tradition along with the exploitation of a wide variety of local mineral and vegetal resources. This is evidenced by a system of sites that demonstrate both special-use activities and long-term habitation (Believa 2004; Hoffecker and Baryshnikov 1998).

Not only do these assemblages resemble others in eastern Europe and the Levant (Golovanova and Doronichev 2003: 129-134), but the stratigraphic contexts at Mezmaiskaya and the other North Caucasian sites suggest that Neandertals and/or other

¹⁷ The Neanderthal infant from Layer 2 at Mezmaiskaya 2 has been directly dated to 39,700 ± 1100 BP (Pinhasi et al. 2011).

archaic humans survived in this isolated area into the Upper Paleolithic or even later (Baryshnikov et al. 1996; Hoffecker 2002: 143; Soffer 2001: 236-244). These observations raise the question as to whether Neandertal populations came into contact with anatomically modern humans once the recession of the Manych-Kerch-Spillway (12.5 – 12 KYA) permitted it, and which cultural and biological traits, if any, were exchanged between them. However, some recent re-dating of materials from Mezmaiskaya indicates that Neanderthals were no longer present there after 39 KYA cal BP (Pinhasi et al. 2012). Nonetheless, Dolukhanov et al.'s (2009: 13-14) assessment of radiocarbon dates for Khvalynian deposits on the Caspian coast of Daghestan and the Lower Volga region suggests the paucity of Upper Paleolithic technologies and extended survival of Mousterian technologies in the North Caucasus, as well as in vast parts of northern central Asia.

Although very few Upper Palaeolithic sites exist either in the North Caucasus or in Central Asia prior to 12 KYA (Dolukhanov et al. 2009: 2), it is a different matter in the South Caucasus. The earliest clearly Upper Paleolithic materials there are known from the Imereti region of western Georgia, where a great number of the Middle and Upper Paleolithic sites are clustered (Ortvale Klde rockshelter, Dzhruchula Cave, and Bronze Cave being the best excavated). At Ortvale Klde, Adler et al. (2006: 95) have established a roughly 30,000-year chronology of Paleolithic occupation from eight main stratigraphic layers (**Table 1**). The Middle to Upper Palaeolithic transition is documented in layers 5-4 (Adler and Tushamramishvili 2004: 102), and therefore seems to have occurred sometime between 42 – 28 KYA. The dates are further refined to

about 38 – 35 KYA (Adler 2006; Adler and Tushabramishvili 2004; Meshveliani, et al. 2004), which is several thousand years later than at established sites in Central and Western Europe, such as Willendorf II (Damblon et al. 1996) and Bacho Kiro (Kozłowski 1988; Kozłowski and Ginter 1982). Interestingly, settlements across the Caspian in the Aral Sea basin date to 50,000 – 35,000 YBP (Boroffka 2010: 285). It therefore seems likely the westerly migration along the Mediterranean coast into Europe (Kuhn et al. 1999) bypassed the Caucasus all together.¹⁸

Layer	Approximate Dates (YBP Cal)
2	20,000
3	23,000
4	37,500 – 28,000
5	42,000 – 39,000
6	44,000 – 42,000
7	44,000 – 41,500
9	47,000
10	48,000

**Table 1. South Caucasus Upper Paleolithic chronology
(Adapted from Adler et al. 2006).**

Besides Ortvale Klde, there are no known sites in the Caucasus in which the Middle to Upper Paleolithic transition is visible. However, the evolution to advanced Acheulean technologies in the Caucasus can be seen in a comparison of three sites.

¹⁸ Adler (2006: 95-6) suggests the reasons for a delayed expansion into the Caucasus (both South and North) and Crimea could have been low population densities, unfavorable climatic or environmental conditions, and perhaps the presence of entrenched Neanderthal populations that were not easily uprooted. It may also have been attributable to patterns of game dispersal. If, indeed, anatomically modern human arrival in the Caucasus occurred late compared to that for the European subcontinent, then the transition would appear seamless.

These include (1) the so-called pebble-culture in level VI at Azokh Cave (Гусейнов 1985), (2) the archaic phase visible at Ignatienkov Kutok, a Black Sea coastal site near Tuapse in Krasnodar (Величко et al. 1965), and (3) the well developed Acheulean industries of western Georgia. As we have already noted, several researchers (e.g., Otte et al. 1995a, b) have pointed out that the Acheulean assemblages with hand-axes very much resemble those of the greater Near East, as it was with earlier Acheulean and Mousterian materials. This continuity of culture is especially important when compared with the areas west and north of the Black Sea during the same time period. In those regions, the lithic industries contain flakes with some core-chopping tools. The areas between the Carpathians and the Don River have yielded microlith-type industries similar to those at Bilzingsleben and Vértesszöllös (Kozłowski 1998: 463-4). Kozłowski (1992) also points out distinct similarities between the Mousterian of the Zagros and the northern part of the Fertile Crescent and that of the Črvena Stijena [Crna Gora]-Karain E type in Montenegro (Баслер 1975).

This Near East-Caucasus trajectory spans what appears to be the entire Paleolithic. It does not in itself, however, suggest anything more than geographic and environmental preference on the part of migrating populations. However, two important points must be made. First, the tool assemblages of the western Black Sea region, and their absence in the Caucasus, would seem to indicate the lack of human migration or diffusion from these regions east of the Black Sea. Second, the continuous habitation of some sites in western Georgia, one even from the Middle Paleolithic to the Neolithic, suggests the possibility of population continuity, hence, ancient gene pools

emerging and persisting there and elsewhere in the region. Here, it should also be noted the concomitant lack of affinity between the Caucasus Paleolithic assemblages and those of Central Asia, which are very diverse in character (Vishnyatsky 1999: 112).

Figure 8 shows the overlapping continuity of western Georgian sites from the Middle Paleolithic to the Neolithic. Of the four sites demonstrating cultural continuity in successive layers from the Upper Paleolithic into the Epipaleolithic, one, Kotias Klde, continues the trend into the Neolithic.

Middle Paleolithic	Upper Paleolithic	Early Mesolithic	Middle Mesolithic	Late Mesolithic	Neolithic
<u>Ortvale Klde</u>					
	Devi-skhvreli: Sakazhia: Mgvimeyi: Sagvardzhile: Samer-Tskhleklde: Svantasavane				
	Dzudzuana Edzani				
	Kvatchara				
	Apiancha				
	← <u>Kotias Klde</u> →				
		Iashtkhya: Entseri: Barmaksyzkaya: Zurtaketi			
		Dzhampala			
			Khupyimshakhya Grotto; Atsinskaya Cave		
			Darkveti		

Figure 8. Paleolithic to Neolithic transition in western Georgia (Constructed from data in Adler et al. 2006, Kushnareva 1997, and Meshveliani et al. 2004)

The appearance of numerous Upper Paleolithic technologies in the European subcontinent cannot be easily glossed onto a pattern of human migration and settlement

as determined by phylogeography. However, some very general patterns have been identified, both in terms of genetics (Cortés Sánchez et al. 2012; Richards et al. 1996; Skoglund et al. 2012; Torroni et al. 1998) and patterns of lithics and other physical remains (Anikovich et al. 2007; Higham et al. 2014; Prat et al. 2011). The very early appearance (c. 40,000 BP) of archaic Aurignacian blades and end-scrapers in Bulgaria and elsewhere in the Balkans is crucial here. Kozłowski (1982) demonstrates discontinuity between these Aurignacian tools and the previous industries in this region, suggesting their arrival from another area. This observation would seem to reinforce a westerly migration route of anatomically modern humans (AMH) from the Levant and/or Zagros, through Anatolia, and into Europe. However, until there are sufficient data to confirm autochthonous Aurignacian technologies in Turkey (Kuhn 2002), little more about this may be said.

The Aurignacian does not appear uniformly in the Caucasus. Its pattern of dispersal is thus far unclear, and there have been numerous opinions regarding the affinities of the industries with those of its neighbors. Not surprisingly, it has been compared generally with circum-Mediterranean assemblages, such as those in Algeria, Italy, and the Levant (Замятнин 1935) and more specifically with Levantine assemblages in Syria, Palestine, and Iraq (Формозов 1959; Bar-Yosef and Belfer-Cohen 1996; Belfer-Cohen and Bar-Yosef 1999). Also not unsurprisingly, some formal aspects appear analogous to the Baradostian and Zarzian industries of the Zagros (Бадер 1966; see also Doronichev and Golovanova et al. 2010).

We have already discussed the importance of Ortvale Klde as an Early Upper Paleolithic (EUP) site, to which researchers have attached the approximate dates of 38,000 – 35,000 KYA (Adler 2002, 2006; Adler and Tushabramishvili 2004; Meshveliani et al. 2004; Tushabramishvili et al. 1999). Adler et al. (2008) subsequently estimated the final EUP sequence to end around 26-28 KYA at both Ortvale Klde and Dzudzuana. თუმბრაძემცილი (1962, 1965) interpreted the lithic assemblages at Dzudzuana, along with materials from nearby Samertskhle Klde, as representing a local variant of the western Georgian Upper Paleolithic, noting that layers II7 – II4 strongly resembled the tool-making traditions of the earlier periods of the region. However, this assessment was purely typological, and no radiometric dating methods were available during the time of excavation. Subsequent reanalysis of the materials yielded a date of 14,000 BP for layer II6 for the Upper Paleolithic at Dzudzuana, although this result was presented with some reservations (Bar-Yosef et al. 2010; Meshveliani et al. 1999).

In the North Caucasus, Mezmaiskaya Cave has yielded EUP dates in the range of 37,000 BP (Golovanova et al. 2006), which makes it comparable in age to Ortvale Klde. The abrupt appearance of beads, needles, pendants, and awls made variously of bone, shell, and marine gastropod indicate not only an innovative shift in use of raw materials, but also a shift in symbolic and ornamental forms. Moreover, there is enough similarity to western Georgian materials to indicate a direct connection between these cultures (Golovanova et al. 2010).

As we have already noted, Ortvale Klde is the sole known site in the Caucasus where any semblance of Middle to Upper Paleolithic transition is evident, although

some sites, such as Khergulis Klde and Taro Klde, contain a mixed Middle and Upper Paleolithic inventories (Kozlowski 1969, 1972; Замятнин 1957). By contrast, the transition appears sudden at Dzudzuana and Mezmaiskaya. In fact, at all three sites, there is a marked appearance of fully developed EUP lithic and bone industry, indicating the concomitant appearance of a new biological population (i.e., *H. sapiens*) (Bar-Yosef et al. 2006; Golovanova 2000; Golovanova et al. 2010). Researchers have noted the close formal similarities between the lithics of these three sites and those of the Early Ahmarian of the Levant (Bar-Yosef et al. 2006; Kozlowski 1998; Golovanova et al. 2006, 2007, 2010; Meshveliani et al. 2004), which is also dated to approximately 40-33 KYA (Belfer-Cohen and Goring-Morris 2007). This relationship stands in distinction from other Caucasian Aurignacian tools and to all other known industries on the European subcontinent.

If transitional assemblages are very rare in the Caucasus, then they are somewhat more common in the circum-Black Sea region and on the eastern European plains. Some thirty sites, mostly in the valleys and river basins to the north of the Black Sea, contain Early Upper Paleolithic assemblages, all falling within the date range of 32,000-24,000 KYA (Cohen and Stepanchuk 1999: 291-93; Tushabramishvili et al. 2002). During this period, beginning about 30,000 KYA, the region experienced changes brought about by the Novoevksinsk regression of the Black Sea, which led to an expansion of land links between Crimea and the eastern European steppe (Островски et al. 1977). This event may have allowed, or encouraged, human expansion from seaside to riverine environments. At this time, a broad range of

Aurignacian industries appears, including Mousterian transitional forms and so-called Eastern Gravettian backed bladelets (Cohen and Stepanchuk 1999: 288-90; Krotova 1995, 1996), which Cohen and Gorelik (2000) suggest is analogous to northern Black Sea region transitions before and after the LGM.

There is very little evidence, biological or technological, linking North Caucasus Paleolithic (and subsequent) populations with those of the eastern European steppe. This may again be due to the impasse to human traffic presented by the Manych-Kerch Spillway. Kozłowski (1998: 480) notes that the entire Caucasus region may have been cut off from Europe, except perhaps via the Black Sea littoral, until the end of the last Interglacial. Having said this, Leonova (1994) notes formal similarities between Kamennaya Balka III assemblages from Rostov-on-Don, particularly microliths, and those of the Imeretian Upper Paleolithic (see also Гвоздовер 1967). Similar assemblages from Fedorovka, near Mariupol in Ukraine, are also worth mentioning in this regard (Кротовка 1986). Whether this evidence constitutes a population or cultural diffusion or some other demographic process remains a question as wide open as the frontier between these two regions.

According to some researchers (e.g., Vavilov 1951), the Russian steppe was not environmentally suitable for cereal domestication or stock grazing until the fifth and early sixth millennia BCE. Prior to this time, hunters likely followed game in the area. However, sedentary activity does not appear in the area until the Neolithic of the Near East, Central Asia (Масон 1966a, 1966b; Виноградов 1981; see Мелентьев 1976 for the Seroglazovka Culture, in the Aral Sea area) or the Pontic-Caspian steppe (see

Формозов 1962 and Колосов 1979, 1985 for the Crimean; see Даниленко 1969 and Маркевич 1974 on Bug-Dniester and Sursko-Dnieper; see also Tringham 1971 and Anthony 2007: 141 for chronologies).

For these reasons, it is safer to suggest the Upper Paleolithic transition in all of Eastern Europe and the Caucasus was a process of cultural and biological replacement, perhaps with some small amount of cultural continuity and biological admixture, as in Western Europe (e.g., Sankararaman et al. 2014). Biological variation in the circum-Black Sea region is complex, much as it is in the Caucasus, to which it bears some important similarities, and this variation may possibly correlate with the archaeological record there. The paucity of evidence from Anatolia notwithstanding, there is sufficient reason to believe tool-making AMH took a Mediterranean coastal route through this region from the Near East, into the Balkans, and perhaps both directions around the Black Sea region before later moving into the Caucasus region, both North and South.

We must also briefly consider the possibility of a concomitant westerly movement from Central Asia at this time as another source of genetic and cultural diversity in the region. To this point, Otte and Derevianko (1996) have suggested the roots of the eastern European Aurignacian lay in the Levallois assemblages of the Altai. In support of this view, Central Asia has been considered the possible homeland for Y-chromosome haplogroups P and R (Derenko et al. 2006; Karafet et al. 2008), two paternal lineages that have given rise to numerous other haplogroups commonly seen in the region, with the latter also playing an intriguing part in the peopling of the Caucasus. However, as we shall see, neither the Y-chromosome nor the mtDNA

evidence supports a Central Asian homeland for all but a minority of North or South Caucasus haplotypes.

11b.2. The Caucasian Epipaleolithic

Thus far, we have made a case for long-term hominin habitation in the Caucasus but limited biological and cultural continuity from the Upper Paleolithic. Based on the continuity of certain stone tool industry and habitation sites, mostly in western Georgia, some degree of biological continuity may be found there. The rationale for this case continues into the Epipaleolithic of this region, which lasted from the 10th to 6th millennium BCE (Bar-Oz et al. 2009; Kushnareva 1997), although Golovanova (2010: 300) dates the Epipaleolithic layers at Dzudzuana (Unit B) between 13,830 BP (\pm 100 uncal) and 11,500 ka BP (\pm 75 uncal). During this time, small sites multiply in number along the Black Sea coast¹⁹, in the North Caucasus²⁰ and eastern Georgia, as well as

¹⁹ The Black Sea coastal sites are of two types, cave and open air. In the former group, we can include Khuyinipshakhva Grotto (Соловьев 1961: 11); Кеп Baraz Grotto (Соловьев 1949); Atsinskaya Cave (Крайнов 1958); and Kvatchara, Iashtkhva, Dzhampala, and Darkveti (see Bar-Oz et al. 2009; Небиеридзе 1978; Церетели 1974). The only known open-air Epipaleolithic site is Entseri (Григолая and Церетели 1967) (along with Tsivi and Achara). The sites of Barmaksyzkaya (see Куфтин 1941: 122), Edzani and Zurtaketi belong to the so-called Trialetian Epipaleolithic (see Габуния 1975). To the Imeretian Epipaleolithic belong Darkveti, Sagvardjile, and Chakhati, and, in Javakheti, there are the Vavra caves (Габуния and Церетели 2003).

²⁰ Aside from Chokh, the Epipaleolithic sites of the North Caucasus are scarcely published, and most appear to be extensions of Paleolithic industries with some changes in style and/or raw materials. These include Kozma-Nokho and Mekegi in Dagestan (Котович 1957: 162), Chau-Leget in Ossetia (Любин 1966), and Sosruko Cave, which is not far from Nalchik in Kabardino-Balkaria (Замятнин and Акритас 1957). These sites are contemporaneous with the Epipaleolithic layer at the open-air site of Chokh in Daghestan, which also seems to have had Mesolithic and Neolithic layers (formerly identified Upper Paleolithic layers have now been reassigned to Epipaleolithic in the literature). Chokh is located on a small, sunny terrace in central Daghestan, which is close to clean water and to hunting opportunities, and seems to have supported year-round occupation. The Neolithic layers there have yielded remains of both a wheat strain typical of what presently grows in the region (i.e., one which does not require much water) and goats of a seemingly domesticated variety. These finds have been interpreted as evidence that the Chokh population was engaged in animal husbandry and agriculture in some form, seemingly

along the Caspian coast and in northeastern Armenia. More could likely be made of the Armenian sites, but unfortunately they remain poorly excavated and/or insufficiently reported (Кушнарева 1984; Мартиросян and Мунчаев 1968; Ушрцццццццц 1967). The character of some of these sites does not change significantly from the Upper Paleolithic, but new and distinctive tool types appear—scalene and isosceles triangles, shaped mostly by bi-polar retouch on blades and bladelets—especially in western and central Georgian sites (Bar Oz et al. 2009: 17). Also during this period, there is a noticeable shift in the assortment of hunted game species, implying that new organizational strategies and possibly new tools are being employed, with evidence of ceremonial bear hunting—a long-standing Eurasian cultural practice—also appearing at this time (Bar-Oz et al. 2009: 21-22).

Of the Black Sea sites, two demonstrate cultural continuity from the Paleolithic, these being Kotias Klde and Kvachara, the former also including Neolithic habitations (Meshveliani et al. 2007). The karstic rockshelter site of Kotias Klde, which lies between tributaries of the Kvirila River, east of K'ut'aisi, has yielded a sequence of Neolithic, Epipaleolithic, and Upper Paleolithic levels, with the Epipaleolithic materials being dated to ca. 12,400 – 10,300 BCE by four charcoal samples (Bar Oz et al. 2009: 16-17; თუმბრაძე 1971). The distinctive Epipaleolithic industry at this site was produced by detachment of uni-directional blades and flakes, most of which were apparently manufactured off-site. An abundance of wild boar, piglet, and bear bones bearing human butchery marks indicate the Kotias Klde rockshelter served as a seasonal

independent of these practices around the same time in the Fertile Crescent (Амирханов 1987; Котович 1964).

hunting camp, with most visits taking place during the late spring and early summer. These details, in turn, indicate that the bears were actively hunted rather than slaughtered during their winter hibernation (Bar-Oz et al. 2009: 21).

There are also several Epipaleolithic sites in the interior of Georgia, both along the Khrami River basin in the Trialeti region (mainly Barmaksyzkaya, Edzani, and Zurtaketi) and in the Rioni Valley (mainly Banetura, Chakhati, Kvedi, Sagvardzhile, and Tsona).²¹ These interior sites are roughly contemporaneous with the coastal sites, but their industries demonstrate stunning typological differences. At Edzani, the industry is a mix of Upper Paleolithic and otherwise distinctive geometric styles (Габунія 1974, 1975), and there is a strong reliance on obsidian, unlike the Black Sea sites (Габунія 1964). Recent research at Bondi Cave and Ortvale Klde (Le Bourdonnec et al. 2012) suggests long-distance obsidian trade was being carried out in the Caucasus as early as the Epipaleolithic. It has also been noted that some tools from this region express a level of craftsmanship closer to Neolithic forms (Габунія and Церетели 1977: 34).

The variety of Caucasus Epipaleolithic sites has prompted one researcher (Церетели 1973) to theorize that the lithic variability within the Georgian Epipaleolithic reflects diachronic trends of development. He suggested a tripartite

²¹ Rioni Valley lithics are, like the Black Sea littoral types, made of flint, but formally they resemble neither the Black Sea nor the Trialeti industries (see ბერძენიშვილი 1964; Каландадзе 1965). However, most of these cave sites (e.g., Kvedi, Tsona, Banetura, Sagvardzhile, Chakhati) remain less thoroughly investigated (see ბერძენიშვილი 1964; Каландадзе 1965). Kushrareva (1997: 9) suggests the Black Sea and Trialeti types do share some formal similarity, whereas the Trialeti greatly differs from both of them. Contemporaneous Epipaleolithic industries in Azerbaijan (for Gobustan see Формозов 1969; for Kichikdash see Мурадова 1979, Рустамов and Мурадова 1971) are also isolated from the Georgian Epipaleolithic industries, as are evidently those of the North Caucasus (for a classic survey see Формозов 1963, 1965: 55).

chronological subdivision for this period of the Black Sea littoral. However, this model was based mostly on typological characteristics of the assemblage and not supported by radiocarbon data. According to this schema, the earliest Epipaleolithic assemblages are characterized by the continuation of Upper Paleolithic traits, with notable increase in flint microlithic triangles, backed bladelets and points. By contrast, the Middle Epipaleolithic phase (based exclusively on materials from Dzhangpala) is dominated by lunates and trapezes, with triangles and points beginning to disappear. In the final stages of the Epipaleolithic, lunates continue, trapezes become more numerous, and the old backed bladelets disappear almost entirely (წერეთლი 1973; see also ნებოეროძე 1975).

The slow transition to food production represents an epochal change in the social order of the greater Near East. However, the timing and process through which this took place remains vague in several regions, including the Caucasus. To assess the points of origin and dispersal ranges of domesticated plant varieties and animal breeds, concerted paleobotanical and paleobiological studies of Chokh²² and other early Near Eastern food production sites should be undertaken. Existing archaeological and

²² Researchers have identified an incredible variety of domesticated grains at Chokh, including single-grained wheat (*Triticum monococcum* L.), emmer [*T. dicoccum* Schrank], and bread wheat [*T. aestivum* L. and *T. compactum* Host.], three species of barley, oats, millet, legumes, etc. (Лисицына 1984a, 1984b, 1984c). Even without detailed comparative archaeobotanical analysis, this observation would suggest it could not have been the only farming location in the region. Indeed, there are other Neolithic- and Eneolithic era sites in Daghestan (see Гаджиев 1980 for Arkhinda, Malin Karat, Muchu-Bakhil-Bakli and other so-called Rugudzhinsk sites; the Tarnair and Buynaksk sites), but most are dated by tool style only, not by floral and faunal remains. Ginchi, a single-culture site dated to the fourth millennium BCE, is characterized as a definitely local early Eneolithic culture whose great variety of stone and ceramic finds (some apparently imported from an unspecified region outside the Caucasus) indicating continuity with earlier local cultures (see Гаджиев 1966, 1974, 1975, 1978, 1980, 1981, 1987). There are also Eneolithic sites in mountainous Georgia (see Чартолани 1974, 1984 and Григолия et al. 1971 for Dzhidzhoeta, Nagutin, Lebkv, Zhirsuki, and Zurakho) and in the Armenian highlands (see Chataigner 1995; Մարդարյան 1967 for Artik, Barazha, and Zaga), but none are well published.

paleobotanical evidence from several sites in the Fertile Crescent, Iran, and Anatolia—in very close proximity to the Southern Caucasus lowlands—indicate a concurrent appropriation of plant and animal materials in the Late Epipaleolithic (see Zeder 2008, Zeder 2011, and Arbuckle et al. 2014 for general analysis; see Coon 1957 for Belt Cave and Dam-Dam-Chechme II; Hole et al. 1969 for Ali-Kosh; Leroi-Gourhan 1969 for Shanidar; Helbaek 1972 for Umm Dabaghiyah; Hopf 1969 for Jericho; Braidwood et al. 1981 for Çayönü Tepesi; and Mellaart 1970 for Hacilar).

Regarding the affinities between Epipaleolithic tool industries of the Caucasus and other sites in the greater Near East, we can say very little at this point except that, as microliths, they are quite distinctive, and in a few isolated cases vaguely Gravettian (Kushnareva 1997: 5). This pattern contrasts with the abundant Upper Paleolithic industries, whose general Aurignacian character has sparked a lively discussion over the range of affinities with the industries of neighboring regions (see Формозов 1959 on affinities with the Levant; Бадер 1966 on affinities with the Zagros; Амирханов 1986b on affinities with the Aurignacian-Perigordian phenomenon; Kozłowski 1998 on affinities with the Early Ahmarian of the Levant; Doronichev and Golovanova 2010 for a review).

In terms of population histories, there is little to tell us about new or continued migrations into or out of the Caucasus during this time, which can, especially in the North Caucasus, be viewed essentially as an extension of the Upper Paleolithic. The apparent dearth of Epipaleolithic-era sites in Armenia and Azerbaijan, as well as in

eastern Anatolia, may reflect a more mobile way of life on the Southern Caucasus steppe, or instead indicate that more survey work is needed in these regions.

Iib.3 The Caucasian Neolithic

If, indeed, the Caucasus Epipaleolithic was underpopulated, despite an abundance of resources, then it did not remain so for very long. Between the 6th and 4th millennia BCE, scores of Neolithic sites appeared across the Caucasus landscapes (Kushnareva 1997: 6-7, 13, 46-48). In the Near East, specifically the Levant and the southern fringe of Anatolia, evidence of early Neolithic domestication dates to as early as 10,000 BCE (e.g., Chikhi et al. 2002; Gronenborn 1999; Gupta 2004; Pinhasi et al. 2005), and slightly later in other parts of the Fertile Crescent. It seems to have spread from Anatolia into Greece and the Balkans by 8000 BCE, and from there into Central and Western Europe, where early sustained agricultural settlements date between 5000 and 3000 BCE (Clark 1965a, 1965b; Zeder 2008, 2011). It has been suggested many times (Ammerman and Cavalli-Sforza 1984; Battaglia et al. 2009) that this so-called Neolithic ‘wave of advance’ did not play an important role in the peopling of the South Caucasus—or even bypassed it altogether. However, increasing evidence from various sites in Armenia (Badalyan et al. 2010; Bălăşescu et al. 2010), all corners of Georgia (Kiguradze and Menabde 2004), Kamiltepe in Azerbaijan (Helwing et al. 2012), and, of course Chokh in Dagestan, indicates that food production either developed locally or was introduced through cultural contacts with farming groups (Renfrew 1991).

In spite of environmentally imperfect conditions for food production, several sites along the Black Sea coast have yielded evidence for agriculture and/or animal herding (for Anaseuli I and II see ბებოჯროძე 1972; for Chkhoroli see Бердзенишвили et al. 1980, Каландадзе 1973; for Kistrik see Соловьев 1967; for Konobili see Пхакадзе et al. 1982; for Odishi see Каландадзе 1939, 1969). The earliest known agricultural settlements in Georgia, Arkhulo I and II, are dated to the 6th millennium BCE (Лисицына and Прищепенко 1977; Rusishvili 1991). From microfloral remains, there is evidence for the use of several different cereal grains. At Shulaveri Gora in southern Georgia, *Vitis vinifera* pips are attested possibly slightly earlier (Кигурадзе 2000; Рамишвили 2001). Elsewhere in the South Caucasus during this time, and in the millennia to come, there occurred a complex and gradual turn towards ploughing technology and irrigation, herding practice, innovative architecture, ceramics, rudimentary metallurgy (somewhat later), and other crafts, and general social productivity.

Between the 6th and 4th millennia BCE, the Kvemo-Kartli and Ararat plains, the Alazan river valley, the Kura-Araxes lowland, Karabakh, and the Muğan steppes in Azerbaijan were settled by what appear to have been extended families or *oikoi* who set up 10 to 15 km from one another (Ессен 1963; Чубинишвили and Кушнарева 1967; ჯაფარიძე and ჯავახიშვილის 1971; Кушнарева 1974, 1977; Мунчаев 1975, 1982; Нариманов 1966, 1982). According to Kushnareva (1997: 21), at the acme of this period, the number of permanent settlements of this type in the South Caucasus, now preserved as tells of the Ancient Near Eastern type, reached 150, and were totally

isolated from the other known food-producing cultures of that time, except possibly for some Late Neolithic/Early Eneolithic settlements on the Ararat plain (Kohl 2007: 68; Lombard 2003; Badalyan et al. 2004; Helwing et al. 2012). North of the Kura, the settlements thinned out and were of a different character (Кушнарѳва 1974). One of these settlements was discovered at Kyul-Tepe, near Nakhichevan, beneath a Kura-Araxes site, which, to some researchers indicates the possibility of cultural continuity between them (Абибуллаѳв 1982; Ессѳн 1963; Кушнарѳва and Чубинишвили 1963).

The settlement tells are associated with two distinct but geographically overlapping Neolithic cultures (Chelidze and Chikovani 2008: 30). The first, arising in the 6th millennium, is known as the Shulaveri-Shomu Culture (5500-4500 BCE), which is thought by some to be the progenitor to both the Kura-Araxes culture and the Trialeti culture in the same general areas of southern Georgia (კობუღრაძე 1976; Kiguradze and Menabde 2004; Кавтарадзе 1983), although Kohl (2007: 68) categorically disagrees with this view. The ceramic Shulaveri-Shomu followed a lesser-known aceramic Neolithic culture, whose transition from Epipaleolithic cultures (circa late 7th millennium BCE) we see only at Darkveti rock shelter (ნებიღროძე 1978).

The Darkveti rock shelter has been of great interest to researchers inasmuch as it demonstrates cultural continuity from the Georgian Late Epipaleolithic into the Neolithic and even Early Bronze Ages. The Late Epipaleolithic layer contained a variety of animal bones along with triangular inserts, microblades, and other lithics. The Early Neolithic layer atop it contained, significantly, microblades and scrapers in

the Epipaleolithic tradition along with more typical Neolithic artifacts such as a polished axe, horn artifacts, and the bones of domesticated animals (ნებოეროძე 1978).

Given only one site with continuous occupation from the Upper Paleolithic into the Neolithic, and a few Epipaleolithic sites with overlapping occupation in either direction, it is interesting to speculate whether the Epipaleolithic to Neolithic transition in the Caucasus was an example of independent cultural evolution (for Chokh, see Амирханов 1987; for Georgia, see ნებოეროძე 1972, 1986; კიგურაძე 1976) or part of some kind of diffusion process from neighboring regions (i.e., Anatolia and the Levant) (Kiguradze 2001). Questions about Neolithic agricultural practice in the Caucasus are important, but not answerable in the scope of this study. Given both the extent of the Paleolithic and Epipaleolithic assemblages and the long-term continuity of Kotias Klde, the continuity of populations in Georgia is likely. Whether agricultural practices developed independently in the Caucasus or arriving with slow spreading Anatolian or Levantine farmers, or through some other form of interaction, will not be known until detailed archaeobotanical studies have been conducted. The proliferation of Early Neolithic sites in the Caucasus could indicate that numerous scenarios are involved.

The Shulaveri-Shomu horizon is thought to have emerged some time in the early sixth millennium BCE (Кавтарадзе 1983; Kiguradze and Menabde 2004; for Aratashen, see Бадалян et al. 2005). Its earliest traces are visible in layers IX – IV at the type-site of Shulaveri Gora in Kvemo-Kartli (southern Georgia) (Kushnareva 1997: 22). The early phase of its ceramic industry is characterized by rough, handmade grey egg-shaped vessels fired at low temperatures, sometimes including sand, basalt chips, or

chaff in the fabric. Various ceramic vessels and implements (such as polishers) from this phase are analogous to materials at Çatalhöyük (layer 5 and on), Hacilar, Hassuna, and Jarmo, and some sites in the Caucasus such as Samele-Klde Cave (Кигурадзе 1986). In addition, an antler sickle with a groove for holding inserts found in the lowest layers of Kyul-Tepe I strongly resemble one recovered at Hacilar (Нариманов 1982: 25).

Two types of pottery distinguish the middle phase of the Shulaveri-Shomu ceramic period. The first is a poorly fired grey-brown or grey-black ware without any organic materials in the fabric, while the second is a well-fired, thin pinkish ware, of various forms and sometimes polished. Most of them featured grooved decoration consisting of fishbone, wave, or other geometric patterns on the shoulders. Again, the ceramic typology and polisher style resembles (and in some cases is identical to) ceramics from both the Neolithic sites of western Georgia, such as Odishi, Anaseuli II, and Chkhortoli, and other Neolithic cultures of the greater Near East, such as Çatalhöyük, Hacilar, Hassuna, and Ubaid (Кигурадзе 1986; Kohl 2007: 67-70).

In the final phase, there is no grooved decoration at all in any type. The thin pinkish wares become more common, along with better-fired grey-brown and grey-black wares with organic materials in the fabrics. Again, a pattern of local and greater affinities is observed. Also at this stage, the appearance of systematic architecture and settlement planning is noted (Кигурадзе 1986; Kiguradze and Menabde 2004).

Material culture from the settlements in Azerbaijan belonging to the same period and later phases (e.g., Baba-Dervish I, Gargalar-Tepesi, Shomu-Tepe, and Toyre-Tepe)

likewise demonstrates affinities with those of ‘Ubaid, Hassuna, and others (Нариманов 1982, 1987, 1992; for Ovçular Tepesi and Nakhchivan, see Marro et al. 2011).

Whether the Shulaveri-Shomu tells, ceramics and implements, with their clear Mesopotamian affinities, suggest the arrival of outside populations or just their ways of life is germane to the question of Neolithic-era changes in genetic diversity in the Caucasus. Kohl (2007: 68-70) argues that this culture represents the arrival of food-producing settlers in Transcaucasia, presumably from Anatolia or northern Mesopotamia. Furthermore, on the basis of the ‘clear disjunction’ between Shulaveri-Shomu practices and choices of raw materials, and those of the subsequent Kura-Araxes culture, the people of the former culture must have assimilated into the local population and otherwise disappeared from the archaeological record (although not necessarily the genetic record).²³ The question of why an archaeological horizon seems to come to a sudden end is always mysterious but, since many local wares and styles were present at Shulaveri-Shomu sites, it is possible the people were exchanging more than goods with the local populations.

The second major Neolithic horizon of the Caucasus, overlapping with the Shulaveri-Shomu and arising in the 5th millennium BCE, is known as the Sioni Culture. This less well-known but seemingly distinctive culture is named after the type-site in southern Georgia and distributed across lower Kvemo, Shida Kartli, and Kakheti in the southeast. Its ceramic industry was produced in a variety of colors, including pink-

²³ If even 100 oikoi were settled in the Kvemo-Kartli and Ararat plains, the Alazan river valley, the Kura-Araxes lowland between the sixth and fourth millennia BCE, their descendants today would number several hundred lineages.

brown, dark brown, red-maroon, chestnut, and black. Vessel types were also more varied than the Shulaveri-Shomu types, with pots (some very large), jars, basins, pans, and bowls being produced. Jars in a variety of heights, as well with a variety of neck, handle, rim, and decoration styles were also attested (Chelidze and Chikovani 2008: 28-29). Kiguradze (2000) and others have claimed that the Sioni horizon is the direct ancestor to the Kura-Araxes culture, although this is a difficult claim to make given that there is no definite point of origin for this vast cultural horizon, only part of which is overlapped by Sioni materials (Kohl 2007: 70). Nevertheless, we must also pause to consider the affinities of Sioni and the pre-Maikop Meshoko settlements of the North Caucasus with northern Mesopotamian cultural elements, particularly Haçinebi Phases A and B (Lyonnet 2007: 150), which would make this a pre-Uruk expansion phenomenon.

In the North Caucasus, the transition from Epipaleolithic to Neolithic stone tool sites (at which local barley and wheat varieties are known to have been domesticated) appears to have been more gradual (see Масон 1982; Бжания 1996). With or without the exception of Chokh, there appears to have been more direct cultural continuity from the Upper Paleolithic through the Neolithic (Bader and Tsereteli 1989; Бжания 1996). This and other related quandaries remain unapproachable until more archaeological work is carried out in the mountainous regions of the Caucasus (that is, as opposed to the steppes and foothills). It is quite possible that the highland and lowland peoples may have for millennia dwelled separately and thus without significant interaction admixture.

Whether these mixed indigenous/greater Near Eastern archaeological horizons and cultures also represent increased biological diversity through admixture is not clear, although explanation for them have long been sprinkled with assumptions about mass migrations. Although the concept of ‘migration’ is largely gone from fashion, changes in genetic lineage frequencies during this period resulting from population movements should also not be rejected out of hand, for the reasons suggested above. For example, Chiaroni et al. (2008, 2010) compared the distribution of Y-chromosome haplogroups J1 and J2 with the distribution of rainfall in the region (**Figures 8 and 9**). Based on this comparison, they interpreted the former paternal lineage as representing herders who resided locally with their flocks, whereas the latter represented agricultural innovators who followed the rainfall patterns. Having probably originated in the Taurus foothills of the Upper Euphrates about 31.7 KYA, populations bearing lineages including both J1 and J2, which are thought to have diverged between 24.1 and 18.5 KYA (Cinnioglu et al. 2004; Semino et al. 2004), shifted to an agro-pastoral economy and dispersed.

This scenario alone cannot explain the remarkably high incidence of these two paternal lineages among the Nakh-Daghestani-speaking peoples (proportionally higher than among Middle Eastern populations; Balanovsky et al. 2011; al-Zahery et al. 2003; Semino et al. 2000) or establish a time frame for the arrival of human populations in the North and South Caucasus. However, it reaffirms our basic geographic premise of a porous southern frontier, albeit one too temporally complex to parse without continued high-resolution genetics studies. A discussion of these haplogroups in the context of others is provided below.

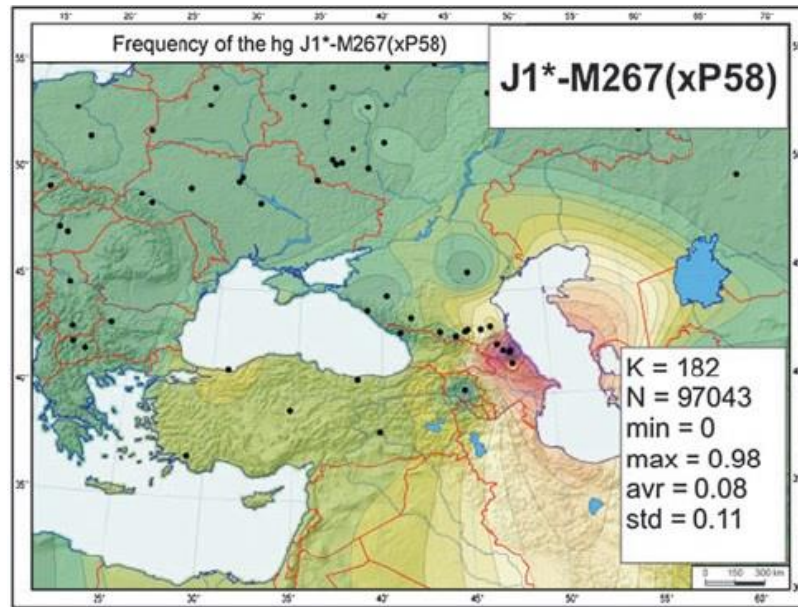


Figure 9. Frequency map of NRY Haplogroup J1*-M267 (Balanovsky et al. 2011)

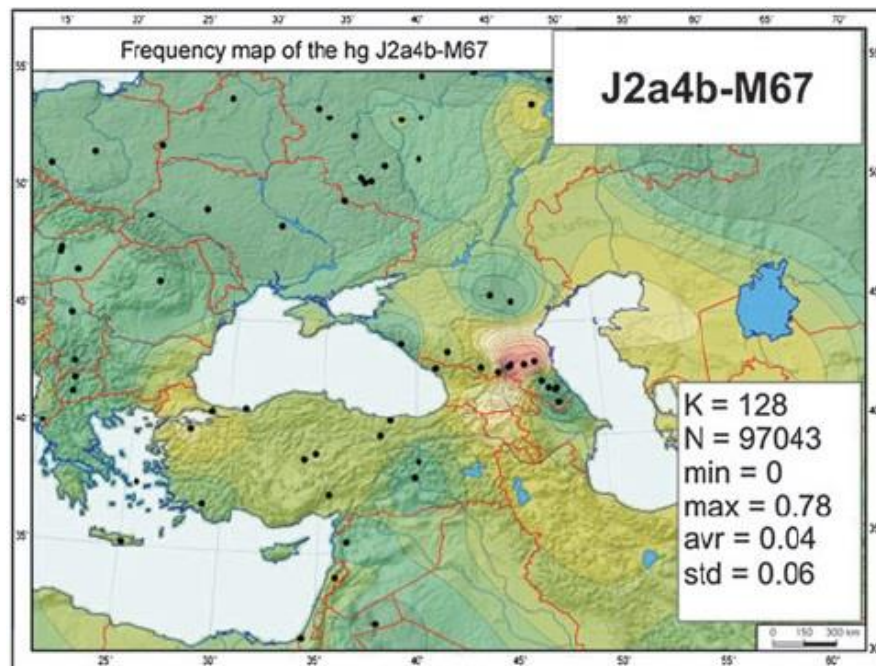


Figure 10. Frequency map of NRY Haplogroup J2-M67 (Balanovsky et al. 2011)

Iib.4. The Caucasian Metal Age²⁴

Of the numerous theories concerning the Neolithic-Eneolithic transition in central Eurasia, the shift in metal procurement sites from the Carpatho-Balkans to the Caucasus is perhaps most relevant to the current analysis. Whether this shift was due to exhaustion of known copper ores, to climatic shifts (Todorova 1991, 1993, 1995, 1998, 2002), to invasions from the east (Telegin 1986; Videjko 1996), or to a combination of such precipitants, is not yet a matter of scholarly consensus. Whatever the reason(s), a “major shift in intercultural relations” began in the middle of the fourth millennium BCE and affected everything around it (Kohl 1997: 53-4). It is at this time that we see the emergence of Balkan coppers and arsenical coppers and bronzes from the Caucasus. Many scholars have proposed ways in which this transition could be related to the concurrent expansion and reorganization of the Mesopotamian world to the south we now call the Uruk Expansion (Algaze 1993; Marfoe 1987; Rothman 2001a, 2001b; Stein 1999; Wright 1972).

The use of metal bearing deposits varied during this transition period. Of the some 400 known deposits and ore bodies of copper, arsenic, antimony, and gold in the Caucasus (Chernykh 1992: 60), most remained untouched until the Late Bronze Age (Kohl 2007: 67). By contrast, Eneolithic ores in the Balkans and cis-Dnieper regions of Ukraine and Romania were being mined heavily at this time (Kohl 2007: 23). Many of the tells of Bulgaria and southern Romania (Spataro 2008), Greece (Τσούντας 1908;

²⁴ This term is used by Soviet archaeologist and metals expert, E.N. Chernykh, as well as other scholars (Chernykh 1992; Kohl 2007), to refer to the complex and overlapping periods of copper, bronze, and iron usage in western Eurasia.

Kontogiorgos 2010) and the former Yugoslavia (Chapman 1989) are, like those of the contemporary Shulaveri-Shomu, Near Eastern in type. Curiously, however, they are rarely stratified beneath layers of bronze, iron, and later materials, as is the case in much of the Near East (Kohl 2007: 23-4; Henrickson and Thuesen 1989). This Western Asia-Eastern Europe cultural trajectory (sometimes referred to as the Balkano-Anatolische Kulturbereich) (Todorova 1998), and its relation to the spread of food producing economies through the 7th millennium BCE and beyond, is well known, if understudied archaeologically. Genetically speaking, however, it has received some recent attention (Chikhi et al. 1998, 2002). Regardless of the directional or sporadic nature of cultural transformation in this large geographic area, the proximity to the metal sources in the Caucasus must be noted.

Long-distance exchange in central Eurasian metals seems to have begun in earnest during the 5th millennium BCE (making these processes coincident with the Eneolithic materials discussed above). During this time, a southeast Europe metals-based cultural trajectory that Chernykh calls the Carpatho-Balkan Metallurgical Province (CBPM) (as well as its inheritor, the Circumpontic Metallurgical Province) supplied the populations of the surrounding regions with vast quantities of copper for tools and weapons, and ornamental gold. The CBMP was a conglomeration, or ‘province’, of distinct archaeological cultures all linked by a shared tradition of mining and forging metals, which dates back to the 6th millennium BCE (Chernykh 1992: 48-53; Pernicka et al. 1997). Chernykh (1992: 48-53) defines three major independent Eurasian metalworking centers, including southeastern Europe, the Caucasus, and

Central Asia, particularly Turkmenistan. According to Chernykh (1992), these three regions developed their metalworking craft largely independent of one another, but also depended on one another at various times for raw materials. At first, it seemed clear that metalworking in the Balkans was far more sophisticated than in the Volga region, implying the metal was arriving there in raw form (Chernykh 1992: 40). However, no ingots have been found in the northeastern periphery region of the CBMP to support this conclusion (Kohl 2007: 38).

Initially, it seems that trade metals were moved from the mining and metallurgical regions of Thrace and Bulgaria, northeastwards through Romania and Moldova, into Ukraine, past the Dnieper, and into the steppe, sometimes as far as the Volga (Chernykh 1992: 50). Much of the copper associated with the Tripolye culture (c. 5500-2750 BCE) of this region has been sourced both to mines at Medni Rid and Ai Bunar in Bulgaria (Pernicka et al. 1997: 141). Presumably, trade links were active both north and south of the Black Sea to customers in the South Caucasus. However, there is as yet no evidence to suggest Caucasus metals played a significant part in the early Carpatho-Balkan-Volga exchange network (Rassamakin 1999). We cannot, for that matter, point to evidence of mining in the Caucasus until the late fourth millennium BCE, during which time arsenic and copper were mined and worked in the South Caucasus and exported north (Kohl 2007: 167). According to Chernykh (1992) only ten arsenic-copper deposits (two or three of which are located in the Caucasus; he does not say which ones) of the 500 Eurasian copper and polymetallic deposits that he examined,

have a “sufficiently high concentration of arsenic for the consistent production of arsenical coppers” (Kohl 2007: 168).

It was during the middle of the 4th millennium BCE that arsenic bronzes were first produced in the Caucasus (tin bronzes did not appear until the end of the third millennium BCE) (Kohl 1995: 1056), thus ushering in the Early Bronze Age of the region. Shortly afterward, the Caucasus came to be a primary supplier of arsenical copper and bronze to the peoples of the Russian steppe. Chernykh (1992: 159-162) has argued that the rise and wealth of the enigmatic Maikop (c. 3700-2500 BCE) may have been due to its position as intermediary for receiving the mineral wealth of the South Caucasus and fashioning it for the needs of the steppe peoples to the north.²⁵ This view may be accurate, but we must also remember how little metallurgical research has been carried out in the North Caucasus proper.

The significance of Maikop lies in its geographical position, which is located along the Belaya River (a tributary of the Kuban) in central Adygea, extending along the east shore of the Black Sea, and to some extent eastward along the North Caucasus barrier. The culture takes its name from a royal kurgan, or ‘chieftain’s grave’, in the capital city of Adygea (also called Maikop). The materials in the chieftain’s grave epitomize the wealth of North Caucasian Early Bronze Age, as well as demonstrating the Maikop Culture’s affinities with both burgeoning Indo-European (i.e., possibly

²⁵ There is very little we can say about Caucasian metals in Mesopotamian contexts, since no wide-ranging spectrographic analysis has yet been performed. With obsidian, this directional movement of materials may be clearer (Kushnareva 1997: 178; Potts 1990: 45). In spite of this, some scholars (see Lyonnet 2009; 2010: 362) have pointed to other examples of north-to-south cultural exchange, such as the firing of pottery in a reduced atmosphere, ceramic polishing techniques, comb decoration, and the so-called Canaanian blades.

Scythian) society (Деген-Ковалевский 1939; Нехаев 1990) and the rather distant Middle Eastern urban centers (see Андреева 1977, 1979; Childe 1936; Ivanova 2007; Мунчаев 1975; Мунчаев et al. 2004; Трифонов 1987; Веселовский 1897), possibly including Iran (Deshayes 1960).²⁶ Мунчаев (1994: 170) suggests that the specific origins of the Maikop culture are to be found in northerly migrations along Tigris, while Betancourt (1970) has noted striking parallels between Maikop copper tools and those of Bronze Age Crete.²⁷

The first cultural phase of Maikop is distinguished from other Bronze Age cultures by its characteristic kurgan burials. Inside them, the deceased were positioned on their sides in semi-fetal position, hands before their faces. Various personal effects such as tools and ceramic vessels were laid around the bodies (Ivanova 2007: 14). Ceramic industries from this phase of Maikop are extremely varied and not yet well collated in terms of their geography or subphases (Мунчаев 1994) (**Figure 11**).

Whatever the relationship between Maikop and the various peoples of the steppe areas, it evidently ended or was culturally diminished during the Transitional phase (see below). There are no new imports or imitations of objects with northern origin at Maikop sites after this time and few stylistic affinities with either north or south are

²⁶ It should also be noted that a number of finely worked local gold artifacts, now displayed at the Georgian National Museum, emerged from excavations of such kurgans in Georgia. From their artisanship, it is reasonable to presume gold was worked there as early as the fourth millennium BCE.

²⁷ His point being not that Maikop copper tools originated in Crete, formally or literally, as has been suggested by Куфтин (1949), but rather that the likenesses demonstrate the vastness of Mesopotamian stylistic influences across the Bronze Age Near East. To wit, Müller-Karpe (1974) notes some similarities between metal bull figures from Maikop burials and those of Horoztepe graves (see Özgüç and Akok 1958).

positively identified. This shift led Ivanova (2007: 22) to characterize mature Maikop as a “center of innovation in its own right”.

The question of the ethno-linguistic identity or identities of the Maikop-Novosvobodnaya cultural community remains open. Were they indigenous peoples managing a transportation center, or instead isolated foreign opportunists following the trail of commerce? If it is, indeed, the case that its intermediate position enriched its inhabitants, then Maikop may have somehow anticipated, or even be chronologically connected to, the steppe kurgan cultures (Belinskij et al. 2000; Chernykh and Orlovskaya 2004). Of the few kurgans shown to predate Maikop, all have clear connections to either Maikop or the Maikop-Novosvobodnaya cultural community, including the little-known Yamna Culture (Rassamakin 2002). Given this evidence, it is possible to consider Anatolian tomb burial sites such as Korucutepe as predecessors to those in the North Caucasus (Trifonov 2004), and probably not vice versa.

Kohl (2007: 58) points out that Halafian pottery is known from several Eneolithic sites in the South Caucasus, such as Kyul-tepe I, which pushes back some form of contact between the peoples of the Caucasus and northern Mesopotamia at least into the 5th millennium BCE. Furthermore, the later megalithic dolmens found along the Black Sea Coast may have been constructed by descendants of the Maikop-Novosvobodnaya culture. If true, then this would allow for the possibility of some permutation of this community to extend at least into the early third millennium BCE (Kohl 2007: 59-61).

Years B.C.	Periodization	Horizon Style	Key Sites
500	Middle Iron Age	Achaemenid	Erebuni, Arnavir
600		Urartu	Erebuni, Karmir-Blur, Oshakan, Aramus, Argishtihinili
700			
800	Early Iron Age	Early Iron II	Horom, Elar, Ketii, Metsamor
900			
1000			
1100			
1200	Late Bronze Age	Early Iron I/ Late Bronze III	Metsamor Artik (group 3) Dvin (burnt level)
1300		Late Bronze II	Lchashen Artik (groups 1-2) Karashamb, Lori-Berd
1400		Late Bronze I/ Middle Bronze IV	Shamiram (burials) Karashamb, Horom, Talin
1500			
1600	Middle Bronze Age	Middle Bronze III	Sevan, Karmirberd, and Karmirvank Horizons Karmir-Berd, Lchashen, Horom, Uzerlik 2-3
1700		Middle Bronze II	Trialeti-Vanadzor Horizon Karashamb (kurgan) Vanadzor (Kirovakan) Trialeti (groups 1-3) Lchashen (120-123) Lori-Berd Uzerlik 1
1800			
1900			
2000			
2100		Middle Bronze I/ Early Bronze IV	"Kutgan" Horizon
2200			
2300	Early Bronze Age	Early Bronze III	Shengavit (3-4) Garni, Dvin, Karnut, Harich
2400			
2500			
2600		Kurs-Araxes Horizon	Mokhrablur Shresh-blur
2700			
2800			
2900			
3000	Early Bronze I	Djervesh (Kurgan 1) Harich (early phase) Keti (burials 1-6) Horom (tomb C1)	
3100			
3200			

Figure 11. Chronology and periodization of Southern Caucasia, 3300-500 BCE (Badalyan et al. 2003)

The question of significant incursions from Mesopotamia, Anatolia or elsewhere into the Caucasus has been raised numerous times without a definitive conclusion based

on archaeological evidence as to their long-term effects on local population history. The presence of Late Chalcolithic-2 (LC-2) and Ubaid chaff-faced wares have long been noted by Caucasus-based researchers (see Lyonnet 2010 for a summary), and many supposed prestige goods of varied Near Eastern provenances are known from North and South Caucasus burials (as seen in the collections of the Georgian National Museum and the Metsamor Museum in Armenia). Among the most compelling lines of evidence for actual cultural and social connections between the Caucasus and the urban centers of the Near East is no doubt the patterning of sites which include distinct, non-local, high quality ceramic vessels.²⁸

Around the turn of the 4th millennium BCE—well before the advent of Maikop—such imported-looking vessels begin to appear throughout western Georgia in a pattern along the Mtkvari (Kura) and Rioni rivers, suggesting a possible northern migration route from eastern Anatolia into western Georgia and the Maikop culture zone (Пхакадзе 1988; Pitskhelauri 2012). The sites along which we trace such a route begin with Ziyaret Tepe, Hanago, Aştepe, and Çolpan in eastern Turkey²⁹. Moving into Georgia, we find materials at the Qvirila Gorge,³⁰ Samertskhle Cave, and Samele Klde (Глонти et al. 1968); Abastumani (see Каландадзе 1974); Orchoshani (ფხვკაძე 2009);

²⁸ Some of which bear close resemblance to vessels from Amuq F and Gawra XII-IX (see Мунчаев 1994: 169)

²⁹ These minor sites are so far known only to contain a few Halaf, Ubaid, or chaff wares among an abundance of local wares (Chataigner 1995: 98-101; Kushnareva 1997: 33, 41; Marro 2007: 78; Marro and Özfirat 2003 and 2005. Ziyaret Tepe and Yılantaş are also discussed at length in Badalyan et al. 2007 and Marro 2008). Though further afield, we should also not neglect to mention the central Anatolian site of Yılantaş.

³⁰ The finds at Qvirila bear certain resemblances both to those at Berikldeebi and at Maikop (Глонти and Джавахишвили 1987a, 1987b; Javakhashvili 1998), though perhaps this matter should not be accepted without further scrutiny.

Dzudzuana Cave (თუმბრაძე 1971); White Cave (i.e., Белая Пещера) [Каландадзе et al. 1976, 1979], Darkveti (Небиеридзе 1978), Samele Klde and Samertskhle Klde (see Глonti et al. 1968).

Pitskhelauri (2012) traces a second possible Uruk-related migration route beginning from the Se Girdan burial mound in northwestern Iran (where Maikop-like materials are attested; see Muscarella 1969, 1971, 2003), north along the shores of the Caspian, and into Daghestan. Among the numerous sites bearing potentially Uruk-influenced materials include Leilatepe, Beiuk-Kesik, Poilo I and II, Misharchaia, Alikemek Tepe, Alkhan Tepe, Chinar Tepe, Abdal Aziz Tepe, Shomul Tepe, Adsiz Tepe, Agil Tepe, and Khodjasan, as well as burial mounds in the Absheron peninsula (see Uch-Tepe, Soyug-Bulag).³¹ While the pattern of these sites cannot be said to establish a long-term biological or cultural continuity between Uruk Mesopotamia and the inhabitants of the Northeast Caucasus, a contribution to an already established phylogeographic pattern is likely.³²

If the presence of so many Mesopotamian-related sites indicates significant migrations—along the riverine systems of the Caucasian lowlands, and the Caspian Sea

³¹ Among the sites in Daghestan mentioned in Pitskhelauri (2012) are Ginchi, Velikent, Toprak-Kale, New Gaptakhm, Serzhen-Yurt, Ust Dzegutinsk, Gorodskoe, Beliaevo, Serker, Miatl, Miskin Bulak, Diubend, and Seidlär (see Гаджиев 1966 and Магомедов 2000).

³² Furthermore, the depictions of a deer and ‘tree of life’ on a cylinder seal from an early Maikop burial at Krasnogardeiskoe strongly resemble late fourth and early third millennium stamp seals from Gawra and eastern Anatolia (see Нехаев 1986). Мунчаев (1994: 189) also notes the curious presence of chipped stone tools in the royal kurgan and relates this practice to the Mesopotamian tradition of depositing such artifacts beneath the floors of temples and public buildings (e.g., at Uruk). Kohl (2007: 75) notes this as well, and considers it significant for determining the “cultural affiliation and formation” of Maikop. Then again, Uruk pottery—such as the mass produced beveled rim bowls, conical cups with string-cut bases, tall water bottles with bent spouts, grey wares, red-slipped pottery, reserved slip ware—is totally absent in the North Caucasus, as are any typical North Mesopotamian artifacts like ‘eye-idols’, tokens, and architectural styles (Ivanova 2007: 17).

coast, respectively—then perhaps Maikop and other cultural horizons of the Caucasus are, in fact, hybrids of indigenous labor and foreign know-how. Such a scenario might explain, for example, the distribution of burial mounds allegedly containing Uruk or Uruk-style artifacts exist in the North and Central Caucasus regions, but not in Anatolia (Ахундов 2010; ჯაფარიძე 2011). An assessment of archaeological materials from Abkhazia would be one of the keys to solving this mystery. In this regard, it must also be mentioned that perhaps not all the newcomers to the Caucasus arrived from the south.

Мунчаев (1994) divides the Maikop Culture into three periods—Maikop, Transitional and Novosvobodnaya—plus an additional pre-Maikop Period recognized by other researchers (Формозов 1994; Ivanova 2007; Трифонов 1996, 2001). The pre-Maikop phase has yielded a distinctive ceramic industry as well as burial customs and miscellaneous finds, which suggest a close relationship with the North Pontic Early Eneolithic cultures. The few available radiocarbon dates date this period to the mid-fifth millennium BCE and later, with possible survivals into the early 4th millennium (Ivanova 2007: 13).

It is during this mid-4th millennium shift in intercultural relations that we also see the rise of what must be the most well known and yet the least understood archaeological horizon in the region, the Kura-Araxes Culture (c. 3500 – 2000 BCE). Sites of its material remains mark a very wide area, including much of Transcaucasus (with the notable exception of western Georgia) and eastern Anatolia (Кавтарадзе 1983; Kohl 2009), plus a fraction of northwestern Iran (e.g., Mohammadifar et al.

2009). Ceramic assemblages in the Kura-Araxes style, known as Khirbet-Kerak wares are also attested in northern Syria and Palestine (Amiran 1965; Greenberg 2007). In addition to pottery, the bases on which researchers have demonstrated Kura-Araxes cultural affinities also include structures (being typically rectilinear, subrectilinear, circular; of mud brick or wattle-and-daub; anthropomorphic and/or zoomorphic hearths, both portable and fixed), well-crafted bone implements and horned animal figurines, and formally fashioned arsenical bronze and obsidian tools (Badalyan et al. 2004: 462; Kiguradze and Sagona 2003).

One remaining question is whether the people of the Kura-Araxes Culture constitute a single ethnic group, as believed by Burney (1958: 178) and Джапаридзе (1969), or instead represent a heterogeneous set of ethnic groups which transmitted this culture into the Caucasus, or perhaps even a hybrid of indigenous and Mesopotamian cultures (Pitskhelauri 2012: 158). It is also not clear whether the Kura-Araxes culture diffused rapidly from a single point of origin throughout the highlands north of the Fertile Crescent, and which culture(s) preceded it. These questions make drawing connections between these various prehistoric Caucasian cultures difficult, especially when considering radical differences such as the classic mud brick building structure of Maikop versus the stone structures of the Kura-Araxes (Kiguradze and Sagona 2003).

Frangipane and Palumbi (2007: 233) see similar continuity from southern Mesopotamia and the northern mountain villages of Anatolia and Transcaucasia in the 4th millennium BCE. They attribute this continuity to “the new and increasing demand of the emerging hierarchies for raw materials, particularly metals”. They further view

the Euphrates urban centers as markets for not only Caucasus metals but also other products. Therefore, many of the Transcaucasian sites, including Shengavit (Rothman 2010, pers. comm.), could have been involved with transporting or working the metal, not to mention other goods such as wine (viniculture; Batiuk 2013).

A great amount of research on the subject of Kura-Araxes identity has been written (see especially Burney 1971; Diakonoff 1984; Kushnareva 1997; Kohl 2007; Pitskhelauri 2012). Kushnareva's (1997) case for continuity between Eneolithic and Kura-Araxes cultures—that the Kura-Araxes people initially dispersed from the southern Caucasus steppe—is beset not only with the burden of its own proof, but also with the problems created by the near simultaneous appearance of Kura-Araxes culture in the South Caucasus (Kohl 1993; Palumbi 2008; Kiguradze and Sagona 2003: 45), Northeast Caucasus (Kohl 1993), eastern Anatolia (Kiguradze 2000; Kiguradze and Sagona 2003), and Syro-Palestine (Amiran 1965; Greenberg 2007). Without a clear pattern of expansion, it is difficult to characterize this phenomenon as autochthonous or intrusive or a combination of both. Viewed over such a wide expanse, it becomes difficult to consider this phenomenon in terms of the expansion of a single ethno-linguistic group. However, as Lyonnet (2007: 12-13) and Pitskhelauri (2012) have pointed out, both the so-called Sioni horizon, which immediately preceded the Kura-Araxes culture, and the pre-Maikop Meshoko settlements are relatable, based on ceramic parallels, to the appearance of Uruk (or possibly pre-Uruk) northern Mesopotamian culture and/or people (Kohl 2007: 70).

While there remains some disagreement over how to characterize populations of the Shulaveri-Shomu, Sioni, Maikop, and Kura-Araxes archaeological complexes, many new sites were settled by people bearing this culture during the early to mid-4th millennium BCE. Beyond those already mentioned, a few additional sites in the Caucasus neighborhood have yielded materials with clear Mesopotamian affinities, although they do not necessarily fall along the two routes we have delineated. These include Kültepe I (Nakhichevan); Leilatepe (Azerbaijan, which does, in fact, fall within the proposed eastern route); Aratashen³³ and Tekhuta (Armenia); and Berikldeebi (Georgia). The three best excavated of these are Leilatepe³⁴, Tekhuta³⁵, and

³³ Aratashen is a minor tell site about which very little is currently known.

³⁴ The site of Leilatepe, in Agdam, Azerbaijan, just to the east of the Nagorno-Karabakh region, is a hill 60 m in diameter and 2 m high, the east edge of which was cut out by a modern irrigation channel (Narimanov 1987). Its habitation area consists of six rectangular mud-brick buildings (built of large bricks), and nine circular two-stage pottery-baking kilns. Three burials of small children in ceramic jars are attested just outside the habitation area (Aliev 1991). Three pottery types are known from Leilatepe. These include (1) chaff ware (the most common), (2) pure clay, and (3) sand-tempered clay. All ceramics are evenly red-baked and the surfaces are well smoothed. The upper parts may have been made on a slow wheel. The surfaces of some of the higher quality ceramics (i.e., chaff and pure clay) have either light green, lemon yellow, off-white, or red slips. Six fragments are painted with designs in black, red, and brown paints. Some vertical stripes are attested, both straight and wavy lines. Most of the vessels are large, round-bodied, open-mouthed, sharply profiled pithoi, but open and straight-mouthed jars with defined lines between neck and body are also known. In addition a few profiled-mouth bowls are described (Aliev 1991). The sand-tempered ceramics are crude, brown-baked, and apparently homemade. Traces of a comb-like tool are noted on some of their surfaces. The vessels are mostly egg-shaped, low-necked jars, some of which bear fine cloth imprints in their interiors (Aliev 1991). Leilatepe pottery may resemble that of Sioni sites, especially late Theluta, early Berikldeebi, and possibly Ginchi (see კიგურაძე 1998)—a notable interregional connection. Leilatepe ceramics have also been linked with the Ubaid culture (Yarim Tepe III) (Aliev 1991; Narimanov 1987). Also in evidence at Leilatepe are some clay objects, such as conical whorls, wheel models, and disks made of pottery fragments, among other items. The residents of Leilatepe were also engaged in metallurgy, as three tetrahedral copper awls, copper wire fragments, and a small copper ingot were recovered there (Aliev 1991). Slag proximate to these metal objects was found to contain 2.1% arsenic and 0.67% nickel. Nickel content is otherwise unknown in Transcaucasian ores. If arsenical copper is present, then it would have presumably been used for alloying copper to make bronze. Moreover, since the slag, drops, and ingot indicated to the excavators that the metal works were located on-site, the population is thought to have understood melting, casting and hot forging (Aliev 1991). In fact, these metal works may be the oldest in the Caucasus.

³⁵ Tekhuta lies on the Ararat Plain, 3 km south of Etchmiadzin. A one-period site, measuring about 1 ha, its cultural deposit begins at about 1.6 m in depth. The settlement included freestanding round structures

Berikldeebi³⁶ and yet are still comparatively unknown, or at least underpublished in any available way. Yet, they are of great importance due to alignment of their dates (roughly 3900 – 3700 BCE). In addition, two of them—Leilatepe and Berikldeebi—are multi-layered sites. Kavtaradze (1999: 69-70) considers them to belong to the final

which were allegedly subterranean or semi-subterranean. Some were apparently habitational, while others were apparently used for storage. Faunal remains indicate the use of domesticated sheep, goats and cattle. Wild boar, red deer, moufflon, bear, and fox were also hunted, while wheat and barley were cultivated (Թրքոյան 1978). Tekhuta was home to a chipped stone industry, mostly obsidian, though some flint is attested. Much of the evidence is comprised of amorphous flakes, although proper tools, such as sickle blades, knives and scrapers, were also found. Three metal objects in particular, a leaf-shaped point and two square shaft awls, suggest inhabitants were competent in metallurgy. It is worth noting the especially high arsenic content of these metals (5.4% in knife; 3.6% in awls), a characteristic of early Transcaucasian metalwork (Селимханов and Торосян 1966). This observation suggests that Tekhuta may have been a site either of simultaneous mixed uses, or cooperation by indigenous inhabitants and Uruk migrants. The ceramic vessels at Tekhuta are either chaff- or sand-tempered, generally yellow-slipped, and sometimes with textile impressions on the interior. Three types were designated by the excavator: (1) crude, handmade, lumpy; (2) well-fired, polished, and usually lustrous; generally small bowls; and (3) black- or red-painted pottery with geometric designs (wavy lines or zigzags) on a yellow or pink surface—perhaps with affinities to northern Ubaid wares (Munchaev 1982; Թրքոյան 1978). Excavators also recovered a type of large chaff-ware jar with a sharply flaring rim—one that is highly important for defining Transcaucasian connections during this period, as it resembles vessels from Tsopi, Berikldeebi, and Leilatepe (Aliev 1991; Javakhashvili 1998).

³⁶ Berikldeebi sits at the junction of the Mtkvari and Pron Rivers, due northwest of T'bilisi (see გოგობო 1997). This multilayered site measures some 4000 m²: 120m x 30m x 3-5m high. The Eneolithic layer is fifth from top, below four Bronze and one Mtkvari-Araks layers (გლონტი et al. 1986; Глонти and Джавахишвили 1987a). Layer V has yielded two types of pottery. The first includes professionally baked and wheel-formed large pithoi, most with 50cm wide mouths, made with purified clay mixed with fine quartz and chaff, suggesting slow-wheel use. The second are medium-size egg-shaped vessels, unevenly baked and formed, made with impure mica-tempered clay, often mixed with coarse quartz (Глонти and Джавахишвили 1987a; Javakhashvili 1998). On the subject of Tsopi, it is worth mentioning the presence there of a quadrangular structure without parallels elsewhere in the Caucasus. გოგობო (1997) believes it to have affinities in religious structures elsewhere in the Greater Near East. Pottery of the first type has been related to that of Leilatepe and Tekhuta, to the Ubaid wares of Tepe Gawra XII-XI, and to pottery at Amuq. Pottery of the second type is thought to be a predecessor or sister type of the Sioni sites (see კვებრიძე 1998). Obsidian, as well as metal tools, are also found at Berikldeebi, although the excavators do not present any obvious indications of on-site metal working. Javakhashvili (1998: 15) compares the Berikldeebi V pottery to that of other Georgian sites, such as Sioni, but Marro (2007: 79) considers these comparisons 'rather loose'. Having studied both the published assemblages (Kiguradze and Sagona 2004; Kushnareva 1997) as well as unpublished Berikldeebi V chaff-faced ware in T'bilisi, Javakhashvili urges caution in all matters of Late Eneolithic pottery comparison in Georgia (see also Marro 2008: 16-8). Square and rectangular mud-brick rooms and multi-cellular structures are in evidence in both Berikldeebi and Leilatepe. This finding again suggests the presence of immigrants from the Near East, as these structures stand out as alien in an architectural landscape where circular single-room houses dominate (Javakhashvili 1998: 11-12, 15; Aliev and Narimanov 2001: pl. II and III).

phases of the mainly 6th millennium BCE Shulaveri-Shomu Culture, whose trajectory covers most of this region.

The alignment of the dates of these three sites, in conjunction with the ceramic wares and architecture at the seven other 4th millennium BCE sites in the region, indicates several trends. First, the chaff-ware and metal-bearing layers of these three sites are nearly chronologically synonymous, prior to which no such wares were known in the Caucasus. This synchrony would indicate the arrival of goods in such containers, if not the permanent residence of Mesopotamians themselves. Second, there is evidence of metal production and use at all three sites, and strong indications of metal working at Leilatepe. Furthermore, as discussed below, arsenic-copper is present at Tekhuta and Leilatepe. Unfortunately, the Berikldeebi reports are not specific as to the nature of the recovered metals. The dates of 3900 – 3700 BCE for metals production are early for this region, and it possibly represents one of the independent inventions of copper-smelting technology, along with that occurring in the Balkans (Radivojević et al. 2010), Mergarh (Jarrige et al. 1995), and Jiangzhai (Wang 2007: 25).

It is difficult to imagine local populations that were still using mostly stone implements suddenly turning to manufacturing arsenical copper and maybe bronze implements. Perhaps the transition was less gradual than we think. Still, it remains unclear how this phenomenon can be connected to commerce with Mesopotamia, although it is worth noting that early metal use and early metal manufacturing seem to coincide at Leilatepe, if not at Tekhuta. It should also be noted that the dates 3900-3700 BCE are nearly contemporaneous with the major North Caucasus culture of Maikop,

which spread from Daghestan to the Kuban River Valley in Adygea, as well as the Tel Khazna I site in northern Syria (see Мунчаев et al. 2004).

In addition to evidence of metallurgy, Mesopotamian-style square and rectangular mud-brick rooms and multi-cellular structures are present at Berikldeebi and Leilatepe, where no such structures were known in the Caucasus prior to this time. The presence of obsidian at all three sites furthers an argument for a growing interest in materials unavailable in Mesopotamia. However, to clarify this situation, we would first need to determine whether Mesopotamian (and/or Egyptian) obsidians originated in the Caucasus, as opposed to Anatolia, where this material is also plentiful (Renfrew and Dixon 1976; see also Potts 1990: 45 for a mention of South Caucasus obsidian present in Arabian Ubaid site Dosariyah). On the other hand, the presence of local and Amuq-F ceramic technologies and styles together suggests cooperation on some level, either in the form of received goods or of settlers.

It is worth mentioning the number of other Late Eneolithic sites in the Caucasus and eastern Anatolia that bear no obvious resemblance to the cultures of Mesopotamia. Marro (2007: 90) categorizes these sites as either Late Sioni or Tilki Tepe. Yet, the locations of the sites may yet prove to be revealing, inasmuch as each lies on a potential transportation corridor. This corridor extended from Tekhut on the Ararat plain, which links eastern Anatolia with northern Iraq to the south; Leilatepe on the Aghdam plain, perhaps along a cis-Caspian route from the North Caucasus; and Berikldeebi also possibly at the foot of a trans-Caucasus corridor from the north, or even in proximity to materials crossing the Black Sea.

These trends, insofar as they are detectable in the Caucasus at a time of relative low population density, present the possibility of a Mesopotamian (or at least Anatolian) element in the peopling and cultural history of the region. What might have attracted Mesopotamian colonists to travel such a distance and perhaps establish a new permanent or semi-permanent home in a strange place? For one thing, the South Caucasus is an area rich in vegetable and mineral resources. While varieties of wheat, barley, and grapes, as well as domesticated animals were abundantly available there, it is unlikely these items would have been the basis for either regular long-distance trade or resettlement outside of the context of commerce. Marro (2007: 91) suggests that Aştepe and Çolpan were seasonal camps for bands of mobile pastoralists, inasmuch as they are single-period sites and located near good pasture. Leilatepe and Berikldeebi are highland sites located between 900 and 1000 meters in altitude, making them relatively similar in climate and topography to Taurus piedmont sites of the Syrian Jezirah and the Upper Euphrates Valley. Therefore, the Transcaucasian region may simply have been part of the Mesopotamian *oikoumenê* (Marro 2007: 91-92).

Each region into which Mesopotamian colonists moved and settled received them a little bit differently (Algaze 2005). By and large, the best-known differences are seen when comparing the Uruk-era settlement areas of Syro-Mesopotamia and Susiana. In the former, the few known 'urban-sized enclaves' are both immediately surrounded by dependent villages and are located at what appear to be strategic positions, whereas in the case of Susiana towns of all sizes were evenly distributed across the landscape. Furthermore, in northern Syro-Mesopotamia, smaller, more isolated Uruk sites existed

far outside this pattern of conglomerated settlements (Algaze 2005: 19). These satellite settlements could have been linked to trade routes extending in and out of the northern plains, Anatolia, and possibly the Caucasus, although Uruk-era relations in this region are dubious.

Mesopotamian-style architecture notwithstanding, it is not possible to determine whether these sites were the result of anything more permanent than trade contact, regular or sporadic, or the circulation of local goods in recycled containers. However, the Eneolithic cultures and subsequent Bronze Age cultures of Maikop (3700-2500 BCE) and Kura-Araxes (3400-2500 BCE), and even Trialeti (2200-1500 BCE), all demonstrate, in their own ways, affinities with cultures of the greater Near East.³⁷ Eneolithic sites in the Caucasus are rare and some researchers do not acknowledge the existence of such a phase (e.g., Akhundov 2004). Based on what little is available (mostly sites in eastern Turkey and southeastern Georgia), Kiguradze and Sagona (2003) mark the dawn and dusk of the Caucasian Eneolithic phase at 4800 and 4000 BCE, respectively (see Smith 2005: 252-4 for a summary).

The Trialeti culture also provides us with a number of novel attributes that have, for several reasons, led researchers to theorize a confluence from the Near East, from Anatolia, and from the steppe north of the Caucasus. Arguing in favor of a Near Eastern origin, Puturidze (2003) cites the presence of large amounts of precious minerals and other materials that reflect a close relationship with the greater Near East. Moreover, she asserts that the people of the Trialeti culture must have been familiar

³⁷ Having said this, it must also be emphasized that the famous Trialeti Cup (as seen in the Georgian National Museum) has no parallels in motif or design.

with the achievements of Anatolian, Sumerian, Aegean, and more distant civilizations and their traditions, although the nature of these ties remains unclear. By contrast, Rubinson (2004: 141; see also Куфтин 1941: Plate 78, top) suggests that Anatolian interaction was paramount based on iconographic affinities between early second millennium Trialeti pottery and Anatolian seals. The similarities of the ceramic wares of these two regions (Rothman 2003) and those of other areas indicate a long-term relationship between them.

While the evidence cited by Puturidze and Rubinson leave little doubt of cultural contacts between Trialeti and the greater Near Eastern world to the south and to the west, perhaps the most convincing evidence of migrations comes from Kohl's (2007) summary of affinities between kurgan typology and wooden wagons on either side of the Caucasus Mountains during the Middle Bronze of Trialeti. Kurgans appear in the Trialeti region of Georgia at this time (mid-3rd millennium BCE), and closely resemble earlier kurgans of similar construction known in the Russian steppe and Caspian plain.³⁸ Also suggestive of movement north to south is the simultaneous appearance of oxen-driven wooden wagons in Middle Bronze kurgans of the Transcaucasus and those on the western Eurasian steppe (Kohl 2007; Chernykh 1992; Mallory 1989). At this time, the entire South Caucasus experienced a wholesale transformation in settlement patterns, apparently based upon the subsistence economy, but also social transformations into milieu and elite, as evidence by the appearance of gigantic kurgans and horse sacrifices in the third quarter of the third millennium BCE (see Badalyan et

³⁸ It is also at this time, around the mid-third millennium BCE, that we have the first evidence for honey gathering at Kodiani (Kvavadze et al. 2007).

al. 2003: 150). The trajectory of the Carpatho-Balkan Metallurgical Province and the expansion of these kurgans (Gimbutas 1973, 1980, 1985) bear resemblances to each other, covering the circum-Black Sea region, the Caucasus, Anatolia, the Volga, and subsequently beyond into Central Asia and Central Europe. Therefore, when reading that Caucasus populations had no significant impact on the populations of the Eastern European plains (Yunusbayev et al. 2012: 13), we must wonder whether the converse is actually meant.

Kohl (2006) views the parallel appearance of similar types of kurgan and wagon on either side of the Great Caucasus as a product of the vicissitudes of socio-economic transition in Eurasia during the second half of the 4th to the 1st centuries of the second millennia BCE. In particular, he cites four “large-scale interrelated and consecutive processes that helped integrate the western Eurasian steppe with areas farther south” during this time period (Kohl 2006: 9). These include the dissolution of the Tripolye settlements and the subsequent need to develop a more mobile economy. This meant, among other things, the driving of “oxen-driven wagons with tripartite wooden wheels across Ukraine and into the pre-Kuban region of the northwestern Caucasus” (Kohl 2006: 9). There was also a disruption of the commercial route of metals “from the Carpatho-Balkan area across the steppes to at least the mid-Volga area” and

simultaneous or slightly subsequent appearance of Early Bronze Age cultures of the Caucasus, particularly the Maikop and Maikop-related cultures of the north-western Caucasus and the Kura-Araxes and Kura-Araxes-related Velikent cultures of Transcaucasia and the north-eastern Caucasus and the subsequent production and exchange of Caucasian arsenic bronzes (Kohl 2006: 9).

A third element of this transition is the “disappearance of Kura-Araxes settlements and the advent of the so-called ‘royal’ kurgans in eastern Georgia’ with wagons, jewelry and possible human sacrifice” (Kohl 2006: 9-10). This shift may have coincided with what Kohl refers to as the various “movements of people into and out of the Caucasus, beginning at the end of the 4th millennium and continuing through the middle of the 3rd millennium BCE”, which would theoretically include the dispersal of Kura-Araxes people into the Zagros and possible into the Levant (Kohl 2006: 9-10). A final process of integration involved transitions in the Bactria-Margiana Archaeological Complex (BMAC) of Central Asia, which is beyond the scope of this study.

Mallory (1989) and others (e.g., Anthony and Ringe 2015) consider the Indo-European *Urheimat*, and thus the point of origin of the wagon and kurgan cultural practices, to be the Ponto-Caspian steppe, from which encroachments clockwise and counter-clockwise around the Black Sea into Anatolia and the Caucasus occurred (see Bouckaert et al. 2012 for a theory about an Anatolian origin of Indo-European). If, in fact, an influx of wagon-and-kurgan people from the Russian steppe journeyed across the Great Caucasus in search of new sources of metals, or for other reasons during a time of economic upheaval, then we might expect that some apportionment of Georgian genetic lineages, especially of the Y-chromosomal variety (Chiaroni et al. 2008), but perhaps also mtDNA, would demonstrate affinities with those of the rest of the Indo-European populations to the north.

Mineral wealth may also have attracted the attention of Mesopotamian noblemen and their smiths. Copper ores are found throughout the Great and Lesser Caucasus ranges and, according to some researchers, the Caucasus was one of the most important centers of early metallurgical development (Kohl 1992: 121). The availability of copper, arsenic and obsidian would have been attractive to Mesopotamian traders and noblemen who could not get such materials at home.

If long-distance trade for small quantities of metals seems far-fetched, then consider the enormous quantity of both tin-bronzes and arsenic-bronzes in the Late Bronze and Early Iron Age, especially in the neighborhood of Ossetia (Kohl 1992: 127). Since such quantities would require regular access to tin, and no tin sources are currently known in the Caucasus or anywhere in the greater Near East except Iran, long-distance trade must have provided these materials to Caucasian foundries. The most obvious source of tin in the ancient world would be Iran, although a Central Asian or European origin should not be discounted out of hand (Cierny and Weisgerber 2003: 23; Dayton 2003; Stech and Pigott 1986) until spectrographic tests on the metal materials can be performed. European tin sources are very few in number and scattered across the subcontinent (Chernykh 1992). Iberian tin was widely traded across the Mediterranean during the Bronze Age (Penhallurick 1986), but it is difficult to imagine the quantities seen in local museums in the Caucasus (to say nothing of the Moscow State Historical Museum) traveling this distance.³⁹

³⁹ One other possibility is quite logical, but underexplored: the Balkans and the Aegean. Several publications (Durman 1997; McGeehan-Liritzis Taylor 1987; Rapp 1999; Skarpeilis 2003) indicate the presence of local tin ingots, as well as geological potential for large ores, but the sources themselves have

Contemporaneous innovation in the South Caucasus involved the Kura-Araxes Culture, whose distinctive black-on-red pottery bears great resemblance to both the black-red polished wares of Syria (Braidwood and Braidwood 1960: 358) and the Khirbet-Kerak wares of Palestine (Greenberg and Goren 2009). The resemblance is so strong that some researchers (e.g., Burney 1958) consider these three assemblages to constitute a single entity. However, there is currently no consensus as to the initial and ultimate trajectories of Kura-Araxes culture, or to its place of origin, and the exact identity of its bearers (see Burney 1958 for an Anatolian origin; see Burton-Brown 1951 for an origin in eastern Georgia and northern Azerbaijan; Кушнарева and Чубинишвили 1970 for an Armenian steppe origin). A comparative analysis of Neolithic architecture in the Caucasus and the greater Near East by A.I. Dzhavakhashvili (Джавахишвили 1973) indicated not only a typological relationship but also a dynamic one.

Although it seems very likely that Mesopotamian traders and settlers made their presence known in the Caucasus during the 4th and 3rd millennia BCE, archaeology alone cannot determine the extent to which they and their descendants affected the course of population history in the Caucasus. Genetic variation is also less helpful in this regard, since it is difficult to distinguish Neolithic and post-Neolithic arrivals

yet to be positively identified, much less spectrographically linked with Caucasian tin-bronzes. Nevertheless, the possibility is most intriguing. What makes a Balkan or Aegean source for tin compelling is the comparison of Late and late Middle Bronze Age materials from Georgia, namely bronze anklets and copper cauldrons (Rubinson 1977: 246-7) with similar materials from the Aegean, particularly the Mycenaean shaft graves. According to Kohl (1992: 128), the affinities are remarkable and indicative of unexplored early cultural contacts between the Aegean and Colchis in the second millennium or earlier (see also Lordkipanidze 1991). The discovery of Mycenaean pottery in northeastern Turkey could be very significant in this regard (Lordkipanidze 1996). This is especially significant because the vessels with honey traces were found in a burial along with arrowheads similar to those found in the Martkopi barrow (see Миндиашвили 2003).

through the distribution of the maternal and paternal lineages alone. Nor without advanced biostatistical methods and additional genetic data can this help us determine whether people arrived in punctuated groups or in a steady stream.⁴⁰

If, in fact, migrants from Mesopotamia settled in sites such as Tekhuta, Leilatepe, Berikldeebi, and others in eastern Anatolia during the early 4th millennium BCE, it is still difficult to estimate the contribution they may have made to the gene pool of the Caucasus. Subsequent demographic changes during the long and tortuous history of this region might have resulted in the total assimilation of the autochthonous populations into that of the newcomers. Moreover, oikoi established by migrants from Mesopotamia (be they farmers or some combination of envoys, traders, and/or laborers from Mesopotamia, possibly with their families, to oversee and record progress of metals fabrication, and/or arrange for the collection and transportation of goods) may simply have disappeared as resources or demand waned. Without more than a handful of Mesopotamian-style structures, the case for settlement at this time remains minimal.⁴¹

⁴⁰ We can, however, make some inferences with linguistic evidence. Since at present there are no surviving indigenous languages in the Caucasus that would link the current inhabitants to the dwellers of urban and rural Mesopotamia, we must look toward Anatolia, where there is a historical presence of Caucasian languages.

⁴¹ One wonders if the best model for Mesopotamian-Caucasus social relations in the pre-Kura Arax period would be, strange as it may sound, Shortughai. This obscure site on the north bank of the Amu Darya in northern Afghanistan was 780 km and 1100 km (as the crow flies) from Harappa and Mohenjodaro, respectively, and yet it was clearly a mature Harappan settlement. This multi-period site, though located in a seemingly isolated area, was in fact part of a broad set of interacting relationships that formed Harappa's external relations, and possibly part of a precursor to Silk Road Trade (as well as a point within the Middle Asian Interaction Sphere) (Possehl 1997). The seeming isolation of the site, Possehl points out, had multiple social and economic dimensions relevant to a study of Leilatepe and Berikldeebi, namely, that it was a Harappan symbol, on the fringes of its trajectory—a positive gesture to its northern neighbors. The living town of Shortughai, by virtue of its location, “brought different kinds of people into peaceful daily contact” and was “a communications node” or proto-embassy, as well as a commercial

The social significance of the various sources of metals in the Caucasus, Anatolia, and the Balkans remains poorly resolved. Who exploited them and on behalf of whom, and how far did such metals travel in various exchange networks? Furthermore, what significance may be made from the presence of the earliest iron smelting sites in northeast Anatolia and western Georgia—both historically Kartvelian-speaking regions proximate to the kingdoms of Urartu and Assyria, who were both consumers of iron and steel?

To take another example, Syunik is rich in metals, many of which continue to be exploited there. Large, deep copper mines exist or have existed in Aygedzor, Dastakert, Kapan, Agarak, Kajaran (where molybdenum is also found) and Vayk; iron is found in Svarants and Meghri (near the border with Iran); and other mineral mines appear in Elpin, Vardenis, and Vayots Dzor. Arsenic, an uncommon but attested metal in the Bronze Age of the Near East, is also present in large quantities in the Meghri region, south of the village of Takhamir. Iron pyrite and arsenopyrite mines are also reportedly found in that region, although no iron smelting sites are currently known there. Arsenic and cinnabar mines also exist in Salvartin, in the Sisian region, not far from Zorats Karer. The lead, gold, silver, and antimony mines now mined in this region were evidently unknown in prehistory (*s.n.* 1967: 156-180, 203-223, 296-299, 316-330, 452-485).

hub (Possehl 1997: 68-9). While Leilatepe and Berikdeebi were not quite the pan-regional centers Shortughai could have been, we suggest the notion of a multi-faceted social center should, in the context of the evidence, be explored more fully.

Given this impressive array of metal sources, and the known surface and burial artifacts from the Sisian region (Есаян and Шагинян 1962; Лисициан 1935; *s.n.* 1898), as well as its geographic location, we might expect this region to be very much a missing link between Early and Middle Bronze Age cultures in the Zagros, Caucasus, and Anatolia (i.e., from the end of the 3rd through the first half of the 2nd millennium BCE). However, owing to unsystematic and incomplete excavations, almost nothing is known about the settlement patterns, relationships of inhabitants, or early exploitation dates of these mineral deposits. Therefore, we can only hope someone will systematically re-examine all the data and continue excavations.

The unique multi-colored vessels appearing alongside local wares in the region by the end of the 3rd millennium may be Hurrian-related (Xnkikyan 2002: 121). Although the eastern boundaries of the Hurrian domain are not known to have included the South Caucasus (Wilhelm 1989: 41), perhaps Hurrian peoples traded for the local metals. Both the multi-colored and local-made vessels seem to disappear around the middle of the 2nd millennium—a phenomenon attributed by Xnkikyan (2002: 121) to the weakening of pan-regional Hurrian influence due to the Mitanni-Egyptian and Mitanni-Hittite wars. In fact, the situation was more complicated, given that Syunik is within the parameters of known Kura-Araxes influence. In addition, a few known Late Bronze Age vessels from the region (e.g., from the Tanzaver cist tomb) seem to retain some non-local motifs while also demonstrating new elements that would later become typical of the Armenian Late Bronze and Iron Ages and beyond (Xnkikyan 2002: 121-22).

The connections (and lapses) between the myths and deities of the greater Near East, from the Aegean to India, have proven to be a very difficult topic to assess. For our purposes, it will be sufficient to note the thick and inextricable links between pre-Christian Armenian motifs and those of the Aegean-Mesopotamia-Iran continuum (compare Black and Green 1998 with Bryant 2001 and Russell 2010). Such does not seem to be the case in Georgia, at least not to quite the same extent, or in the North Caucasus.⁴² The fact that the literature and motifs of Greater Armenia pre-Christian deities have clear Mesopotamian and Aegean cognates is perhaps unsurprising geographically, inasmuch as parts of historical Armenia abut Syro-Palestine and Mesopotamia, and certainly Iran. However, in the Bronze Age era of Urartu and pre- or proto-Armenian identity, this connection is especially worth noting, as it speaks to the very dense Mesopotamian character of this society, and possibly, therefore, to its origins as a population.

Ic. Genetic Variation in the Caucasus

A characterization of the genetic diversity of the Caucasus would seem to be immediately beset by a physical obstacle, namely the mountain range itself. The cultures and languages of the Caucasus, north and south, as well as some within them, could be said to differ as much as Japan, Korea, and China. They are neighbors separated by geographic barriers, and though they share many key genetic lineages and

⁴² Trends in Aegean-Caucasian philology seem to indicate an Anatolian or Black Sea region sphere of common motif and literature (e.g., Prometheus-Amrion). See Braund (1994) and Kurtsikidze (2008) for descriptions.

cultural traits, they differ entirely in other ways, such as language. In spite of the cultural and linguistic differences between the peoples of the Caucasus, there is every reason to believe that the region's rugged terrain has not served to greatly reduce gene flow within it.

The question is whether the current pattern of genetic variation in the Caucasus as a whole was extant well before the formation of ethno-linguistic patterns within it. This is not to suggest there was one and only one migration into the region, after which no one ever entered or left again. To the contrary, certain historically documented incursions by Alans and Mongols, as well as other Altaic-speaking groups, have left genetic and linguistic traces of their movements in diverse Caucasus populations. On the whole, however, the entire Caucasus region may reflect, like its neighbor Anatolia, continental Europe, and perhaps the greater part of the Near East, a genetic landscape well established before the Bronze Age.

The three seminal papers on Caucasus phylogeography—one covering the South (Barbujani et al. 1994), another the North (Balanovsky et al. 2011), and a third both North and South (Yunusbayev et al. 2012)—collectively describe autosomal (diploid) and haploid genetic variation.⁴³ Although spanning seventeen years, the coherence of the basic results of these methodologically diverse papers confirms our interpretation of the archaeological and historical literature.

⁴³ Haploid genetic markers are those inherited either maternally (mitochondrial DNA) or paternally (Y-chromosome, specifically the non-recombining portion). Autosomal markers are those passed on biparentally, and which reflect apportionment from a wider spectrum of ancestral lineages.

Barbujani et al. (1994) conducted a spatial autocorrelation analysis of 31 alleles from blood group, serum protein, and red blood cell enzyme loci in 793 samples collected by Ivan Nasidze from the Russian and Georgian scientific literature.⁴⁴ This analysis indicated high levels of gene frequency differentiation between ethnic and linguistic zones rather than the geographic zones identified by Balanovsky et al. (2011). In other words, the various geographic barriers, including the Caucasus itself, apparently had little influence on the patterns of genetic differentiation there (Barbujani et al. 1994: 660-61).

A second characteristic yielded by this study was the extensive non-clinal genetic variation throughout the region. This finding was interpreted as evidence against a 'wave of advance' settlement pattern, which would have yielded a clinal pattern of variation as seen in the genetic structure of Europe (Sokal et al. 1992; Cavalli-Sforza et al. 1993; Skoglund et al. 2012). It has thus been theorized that agriculture spread into the Caucasus through cultural transmission rather than demic diffusion (i.e., with gene flow), although a limited degree of migration may have occurred (Barbujani et al. 1994: 663). Yet, if, according to Barbujani (1994: 661), seventeen out of twenty-two significant genetic barriers co-occur with linguistic barriers, what can be theorized about the origins of these populations? That they emerged as ethno-linguistic groups *ex situ* and resettled in the Caucasus, perhaps due to

⁴⁴ Each of the 1651 records of the original database included the name of a sampling locality, its spatial coordinates, the sample size the allele frequencies at one locus, and the [presumably first] language spoken by the individuals studied. The final database includes 31 alleles belonging to 17 genetic marker systems, corresponding to an independent locus, with a few exceptions (Barbujani et al. 1994: 642). Unlike the Balanovsky et al. (2011) and Yunusbayev et al. (2011) studies, the markers used in this paper are biparentally inherited.

external pressures? That they emerged *in situ* as linguistic-genetic nuclei and resisted assimilation for millennia?

This question, as it pertains to the North Caucasus, was the focus of the Balanovsky et al. (2011) study, which examined the relationship between linguistic and Y-chromosome diversity in the North Caucasus. Of the four predominant Y-chromosome haplogroups observed in the North Caucasus (G2a1-P16, G2a3b1-P303, J1*-M267[xP58], J2a4b*-M67[xM92]),⁴⁵ each had its own geographic and linguistic domain, outside of which it was infrequent or absent (Balanovsky et al. 2011: 19).⁴⁶ The finding of ethno-linguistic zones was remarkable since it does not have a parallel in Europe or Central Asia, and thus may be largely the product of topography. However, Balanovsky et al.'s (2011) findings do not suggest rigid geographic boundaries, but rather a strong correlation between the Y-chromosome and linguistic data for populations, keeping in mind that language and geography are often closely linked (e.g., Semitic languages; Kitchen et al. 2013). It is also worth noting that, although Caucasian languages have a reputation for, among other things, incredible diversity, certain pairs of languages (e.g., Circassian and Adyghe) are more mutually intelligible

⁴⁵ Y-chromosome haplogroups are defined by single nucleotide polymorphisms (SNPs), or mutations, that are given alphanumeric designations in a system (currently A through T) initially devised by the Y Chromosome Consortium (2002). The first capital letter represents the haplogroup, and the letters and numbers that follow indicate subhaplogroups or subclades, which are defined by the terminal SNP of those branches (e.g., M67 above). Since the cladistic structure of the Y-tree is constantly changing with the addition of new data, the bracketed portion indicates the markers that define the subclade. An asterisk following the haplogroup designation typically designates it as the ancestral node or branch from which new branches arose.

⁴⁶ A more thorough analysis of North Caucasus mtDNA variation is needed.

than others, and thus their speakers are more likely to have exchanged marital partners, ergo genes.⁴⁷

Perhaps the most crucial point not yet fully tested concerns the time necessary for gene- and language-restricted zones to arise. The time required would likely be considerable (though less so if geographic barriers firmly separated populations), given what is known about language evolution and glottochronology (Gray et al. 2011; Warnow et al. 2004). Thus, these four zones may reflect some degree of *in situ* population continuity since the North Caucasian Epipaleolithic and even the Upper Paleolithic, as some archaeologists (Бадер and Церетели 1989) have proposed. Keeping in mind that the phylogeny of Caucasian languages is still very much an open question (Tuite 1999; Klimov 1994), we need not imagine that the languages of Abkhazia, Circassia, Chechnya, and Daghestan originated from a common root language that traveled with various settlers. It may even be the case that three or more unintelligible autochthonous languages or language groups came to share certain features through diffusion at the same time as their essential characteristics emerged (i.e., a Sprachbund), as has been suggested by some linguists (Catford 1977: 312), or more probably through a series of small linguistic areas, some quite ancient (Tuite 1999).

A further reason to consider an early date for the settlement of the North Caucasus is the Chokh site. Although one must certainly wonder why settlers would

⁴⁷ The practice of obtaining brides from other areas (by formal commerce or by theft) is, incidentally, a long-standing tradition in parts of the Caucasus. See Grant (2005) for an interesting overview of how this tradition has played out in Russian ethnographic research and other literatures.

travel so far to such an isolated place in order to produce food⁴⁸ more easily managed in the Georgian lowlands, the presence of this seemingly isolated early site, if accurately dated, does indicate early habitation there. The North Caucasus, therefore, was likely settled by the ancestors of its current inhabitants at the Epipaleolithic-Neolithic cusp, even if settlement and food production per se have emerged and been abandoned more than once. If food production technology arrived in Daghestan and elsewhere in the Caucasus through cultural or demic diffusion, then Iran cannot be excluded as a point of origin, especially given the openness of the Caspian western shore route (Амирханов 1986a: 1-7). The dominant paternal haplogroups of the North Caucasus (G2a1, G2a3b1, J1, and J2a4b) are typically interpreted as evidence for dispersals from the Near East (Balanovsky et al. 2011; Herrera et al. 2011). As we will see, eastern Anatolia and the Ararat Valley may also have served as transit points between the two regions. Furthermore, Y-chromosome G may have arisen in Iran (Balanovsky et al. 2015) and, thus, its presence in the Caucasus will have to be taken into account in explaining patterns of genetic diversity in the region.

The Yunusbayev et al (2012) study extends the view of early human settlement and continuous occupation in the Caucasus in asserting that autosomal DNA identity by descent (IBD) patterns in this region were likely established prior to ethnic and linguistic differentiation.⁴⁹ Overall, this study confirms the lack of a distinct genetic

⁴⁸ That is, unless Chokh does, in fact, represent an independent origin of agriculture unrelated to Fertile Crescent and Iranian highland food production.

⁴⁹ DNA segments are considered to be identical by descent (IBD) in two or more individuals who share common sets of mutations and arose from a common ancestor. Individuals with DNA segments which are identical due to sharing common mutations (i.e., independent mutations) but who do not share a common ancestry are considered identical by state (IBS).

boundary between the Caucasus and the greater Near East. Given the high linguistic diversity of the Caucasus overall, especially in topographically isolated places such as Daghestan, we are left with a view of the Caucasus, like its neighbor Anatolia (Gökçumen et al. 2008; Yardumian and Schurr 2011), as a locus of slow but massive social transformation, but not one of marked by biological replacements. As Barbujani et al. (1994) observe, the fact that very little clinal genetic variation is observed in the South Caucasus could itself be taken as an indicator of demic diffusion, but if so, not due to rapid and massive gene flow. Barbujani et al. (1994: 659) go on to conclude that “genetic drift played a greater evolutionary role than gene flow” in shaping local patterns of genetic diversity in the region, while populations there maintained longstanding genetic differences. In other words, their data argue against the notion of large, discrete migrations from the Near East or the Russian steppe over time, and in favor of smaller-scale and perhaps continuous settlement patterns, the cumulative effect of which would be indistinguishable from a single large expansion.⁵⁰

Related studies of these areas (e.g., Balanovsky et al. 2011; Tambets et al. 2000; Weale et al. 2001; Yunusbayev et al. 2012) have refined Barbujani et al.’s (1994) zonal division model by demonstrating some degree of genetic affinity between South Caucasian populations and populations of the greater Near East. Much of this patchwork quilt pattern remains fundamental, inasmuch as it may have been established

⁵⁰ Such arrivals have introduced statistically recognizable regularities of patterns in Europe’s genetic record (Sherratt and Sherratt 1988).

during the Epipaleolithic or Upper Paleolithic, and later diversified but never deliberately reorganized.⁵¹

Having identified this very basic and perhaps hyperopic trend in the phylogeography of the Caucasus, we will now review the literature on population affinities, and thus refine the understanding of the phylogeographic structure of the region. Given what has been generally observed in the rest of Europe (Balaesque et al. 2010; Cavalli-Sforza et al. 1994; Haak et al. 2015; Lazaridis et al. 2014; Nelis et al. 2009; Paschou et al. 2014; Sokal et al. 1991, 1992; Skoglund et al. 2012) and in South Asia (Barbujani and Pilastro 1993; Chambers et al. 2014; Gangal et al. 2014; Majumder 2010; Metspalu et al. 2011; Reich et al. 2009), a Neolithic-era (or prior) diffusion of Near Eastern populations from the Levant and the Zagros (i.e., in a northerly direction) and steppe (i.e., in a westerly direction) should have produced discernible gradients of gene frequencies (Barbujani et al. 1994). Instead, the spatial autocorrelation analysis performed by Barbujani et al. (1994) reveals a west-east gradient in gene frequencies, suggesting that the colonization or diffusion may have originated in Anatolia rather than from areas to the south (i.e., Syria, Iraq, and Iran).⁵² Since a relatively large number of Y-chromosome and mtDNA haplotypes found in the Caucasus seem to have originated very generally in West Asia, including possibly Anatolia, this region may have served

⁵¹ Both the South and North Caucasus have undergone many demographic transformations and reorganizations in the tens of millennia since the Upper Paleolithic, with many occurring during the 19th and 20th century. Given the mass deportation of Chechens and Circassians from their ancestral homes in the North Caucasus (Polian 2004; Richmond 2008: 84-5) and the Bolshevik-Ottoman gerrymandering in the South Caucasus (Horváth 2011; Цуциев 2005), it is worth wondering to what extent other potentially visible regularities were disrupted or erased.

⁵² However, it must be borne in mind that the level of resolution of Barbujani et al. (1994) is far less than for the more recent studies.

as a genetic reservoir for diverse peoples who moved west into Europe and east into the Caucasus. The dearth of archaeological data from Anatolia's Paleolithic limits many of the conclusions that we might otherwise make concerning the continuity of Paleolithic and Epipaleolithic tool assemblages. However, genetic studies of Anatolian populations indicate they are largely autochthonous in spite of a recent wholesale shift in language and ethnicity (Cinnioglu et al. 2004; Comas et al. 1996; Gökçumen et al. 2008; Yardumian and Schurr 2011).

Genetic data for Armenian populations are remarkable in pointing to their origins in post-glacial eastern Anatolia, not in the Balkans or Iran, as some have suggested (Herrera et al. 2012; Lowery et al. 2011; Nasidze et al. 2003, 2004; Tambets et al. 2000; Weale et al. 2000). This observation is somewhat at odds with long-standing linguistic theories, coupled with literary attestation from Herodotus that Armenian-speakers were, like Phygians, colonists from the west who settled among the ruins of Urartu (Renfrew 1987: 71-3; also see Mallory 1989: 33-4).⁵³ Despite Armenian not being considered an Anatolian Indo-European language but rather a closer relative of putatively Balkans-based Indo-European languages such as Phrygian, Thracian, and Greek (Hubschmann 1967; Martirosyan 2013; Saryan 1992), there is still a case to be

⁵³ The earliest documented presence of Armenians in the Caucasus region (or eastern Anatolia) comes from either the Bitsun inscription of Darius the Great (authored sometime between 522-487 BCE), or possibly from the Neo-Babylonian Nabonidus Chronicle of Cyrus the Great (circa 547 BCE) (Stronach 2007). While we cannot at present determine which branch of Y-chromosome haplogroup E is represented in the Armenian samples, the presence of any E haplotypes is interesting given its general geographic distribution. E1b1b (formerly E3b) (specifically E3b1-M78 and E3b3-M123) is associated with Neolithic expansion into Anatolia by virtue of the consistency of its expansion date with that of agriculturists moving into the area, perhaps multiple times, from the south and west (Cinnioglu et al. 2004). We cannot rule out the western entry of haplogroup E into Anatolia, just as Mallory (1989) has never ruled out a western and/or entrance of Indo-European speakers into Anatolia.

made for speakers of Armenian constituting an intrusive presence from western Anatolia or the Balkans.⁵⁴

However, others (chiefly Diakonov 1985) have made the case for a significant Caucasian substructure consisting of loan words from Kartvelian and Northeast Caucasian, and possible Hurrian and Urartian. If this is the case, then we may need to speak of a gradual linguistic and cultural shift toward Armenian, beginning around 1200 BCE. Such a notion would be supported by the cessation of genetic signals of population mixture observed in Armenian populations coinciding with the collapse of Bronze Age civilizations in the Near East and Eastern Mediterranean (Haber et al. 2015).

The conclusions reached by Herrera et al. (2011) about Armenians origins are also relevant inasmuch as these researchers sampled individuals from the Ararat Valley as well as Gardman, Lake Van, and Sasoun, most of whom now live in abroad. The vast majority of male individuals belonged to one of five Y-chromosome lineages (E1b1b1c-M123, G-M201, J1-M267, J2-M172 and R1b1b1-L23) associated with the

⁵⁴ That Armenian is demonstrated to show closer affinities to Phrygian, Thracian, and Greek, rather than to languages such as Luwian and Hittite, and thus must have shared a common biological ancestry with speakers of the former, and migrated from the Balkans to the ruins of Urartu. Since linguistically this line of reasoning (see Mallory 1989: 33-4; 273-4, note 10) hinges on the assumption that Greek, Thracian, and Phrygian have their origins in the Balkans rather than Anatolia, it has been countered by both Renfrew (1987) and Gamkrelidze and Ivanov (1985), who reverse the model by placing the Indo-European homeland in eastern Anatolia, and the migration direction west into the Balkans, rather than east from the Balkans. Recent research (Bouckaert et al. 2012), which has not gone uncriticized (Pereltsvaig 2012), does at least reposition Anatolia as the possible home of Phrygian, Thracian, and Greek, and thus a more complex, central thesis, shorn of great and convenient migrations, can be devised. A further reason to consider Greek or proto-Greek as an Indo-European language with at least a partial origin in Anatolia comes from E.J. Furnée's studies of Kartvelian-Greek loan words (Furnée 1972: 398-401; 1982). Except in Colchis, Greeks and Kartvelian speakers were not proximate in Anatolia from the Seljuk period on, and likely well before. That Balkan Greek contains Kartvelian loan words is enough to suggest long-term contact in western, central, or even eastern Anatolia.

Neolithic Expansion, and not with Indo-Aryan expansions or with southeastern European populations (Myres et al. 2011; Herrera et al. 2012).⁵⁵ The data themselves are remarkable because they serve to establish a potential interface for Levantine and Caucasus populations, and, in anticipation of conclusions reached by Haber et al. (2015), with prehistoric Europe. These four main Y-chromosome lineages (plus a fifth, the rarer T-M184) comprise a substantial portion of those seen in the Caucasus, suggesting that eastern Anatolia and Armenia may have served as a staging ground for one or more of the critical human settlement events in the region. Unfortunately, studies of equivalent resolution for mtDNA variation in these populations are fewer in number.

It may be worth mentioning that the Epipaleolithic or Neolithic settlers in eastern Anatolia and the Ararat Valley, for whom today's Armenian populations served as proxies, were not Armenians in any sense of the word, any more than they were Georgians, Azerbaijanis, Kurds, or any other modern ethno-linguistic group. Indeed, if we are correct in our assessment that these Epipaleolithic settlers are ancestral to many of the modern South and North Caucasus populations, then they may well have been speakers of a proto-Caucasian, one language or many, which are in complex ways ancestral to Hurrian, Hattian, Urartian, Georgian, and possibly even languages of the Northwest and Northeast Caucasus, although these may also be completely unrelated (see Oštir 1921 for a proposal that the Northeast Caucasian (Nakh-Dagestanian)

⁵⁵ Since the Anatolian Armenians were all but erased from their ancestral homeland there (see Akçam 2006, 2012), a study of Armenian-Americans, as well as diasporan Armenians living in the Middle East, would perhaps reveal even more J1 and J2 haplotypes among them.

languages and Hurro-Urartian languages constitute a single family called Alarodian; a fuller discussion of this topic appears below).

The phylogenetic layout of the Caucasus, as depicted in Barbujani et al. (1994) and Yunusbayev et al. (2012), follows directly from this notion that eastern Anatolia and the Ararat Valley served as an interface, and perhaps source area, for settlers following the retreat of glaciers. Since, as we have established, glacial presence was inconsistent in the Caucasus, the process of settlement may well never have been fully interrupted. Thus, the high levels of allele frequency differentiation between ethnic and linguistic zones (Barbujani et al. 1994: 660-61) may have been a process begun in the late Pleistocene. The non-clinal genetic variation throughout the region, interpreted as evidence against a ‘wave of advance’ settlement pattern, may indeed reflect vestiges of Pleistocene settlement and subsequent cultural restrictions to gene flow.

Barbujani et al. (1994) suggest that diversity among Caucasus populations is great, even between geographically close neighbors, and greater even than among populations of the Middle East and South Asia. Yunusbayev et al. (2012) also suggest that the autosomal IBD patterns in the region were established prior to ethnic and linguistic differentiation. Therefore, we may conclude that some significant portion of the alleles and genetic lineages in Caucasus populations are quite ancient. The influx of populations from the Levant and Anatolia during the Late Holocene and Metal Age, and subsequent social organization processes, are often used to explain both the linguistic and biological diversity there. We contend that this level of diversity can only be explained by a considerable time depth of human occupation in the region, which, by

extension, necessitates the settlement of some portions of the Caucasus during the late Pleistocene.

The fact that the predominant Y-chromosome haplogroups in the Caucasus are G2a, I2a, J1, J2a, R1a, and R1b is unsurprising given that the putative ancestral homelands of these lineages, with the exception of R1a, lay in adjacent regions to the south.⁵⁶ The significance of each of these lineages will be discussed below. The presence of Y-chromosome haplogroup Q among Chechens and Balkars (Balanovsky et al. 2011) also requires further investigation, as does the almost total absence of Y-chromosome haplogroup E (except among Armenians), which is otherwise quite common in all parts of the Middle East and Anatolia (Abu-Amero et al. 2009; Cruciani et al. 2004; Semino et al. 2004).⁵⁷

The mtDNA haplogroup frequencies of the Caucasus are extremely variegated, with every Eurasian haplogroup present except for E, L, O-Q, and S (all of which are exclusive to Oceania and Southeast Asia, or in the case of L, mostly African; Gonder et al. 2007 for L; Hudjashov et al. 2007 for Q; Palanichamy et al. 1994 for O, P and S;

⁵⁶ Haplogroup points of origin are always provisional, inasmuch as they are based upon high concentration and often the general impression that AMH did a lot of evolving in the Near East. But high concentration is of course subject as much to drift (Barbujani and Colonna 2013: 5). A co-examination of the various Y-chromosome and mtDNA frequency heat maps in the literature, we note they form rings or crescents around the Caucasus region but none are thought to have emerged just there.

⁵⁷ Given the range of Y-chromosome haplogroup C as limited to the Northeast and north-central Caucasus, its presence is most certainly related to Mongol incursions from Siberia and Central Asia (Derenko et al. 2010). However, it should also be mentioned that a form of this very geographically widespread haplogroup is known from the aDNA of a 7,000-year-old Epipaleolithic European from northern Spain (Olalde et al. 2014.) Y-chromosome haplogroup Q, like C, has an eastern Eurasian and American trajectory. Its presence in continental Europe and the Caucasus is almost non-existent and therefore unlikely to be a vestige of pan-Eurasian Upper Paleolithic or Epipaleolithic settlement. Y-chromosome haplogroup F, which appears in several older studies (e.g., Nasidze 2003, 2004; Wells et al. 2001), almost always denotes one of its major sub-clades (G, H, and IJK), as F* itself is very rare and even then more often a by-product of lower resolution SNP genotyping.

Friedlaender et al. 2005 for P and Q in the South Pacific; see also Forster et al. 2001). Furthermore, all mtDNA haplogroups with the exception of H* are present at percentages of less than 15%. The presence in the Caucasus of mtDNA haplogroups, such as C and D (each found almost exclusively among Nogais; Bermasheva et al. 2004), is best explained through known migration events relating to the conquests of the Golden Horde and its lesser sequel, the Astrakhan Khanate (Новосельский 1948; Kurat 1961; Pritsak 1967). Nearly 50% of Nogai men possess a Central or East Asian maternal lineage, whereas such haplogroups are all but absent among other Caucasus populations.

As remarkable as these data may seem, many ethno-linguistic populations have not yet been characterized for mtDNA variation (or the data for them are unpublished) or else the mtDNA data exist at such a low resolution that only limited insights into their genetic ancestry can be gleaned from them. In spite of this limitation, the overall picture remains one of great diversity comparable with that observed in Central Asia (Heyer et al. 2009; Martínez-Cruz et al. 2011; Dulik et al. 2011). These facts alone would suggest that the Caucasus is a well-trodden region. Perhaps the most striking, and for now unanswerable, question regarding mtDNA variation in the Caucasus concerns not so much the small percentages of East and South Asian haplogroups which have accumulated there over the millennia, but rather the possible autochthony of mtDNA lineages belonging to haplogroups H, T and U.

Although mtDNA studies of the Caucasus require higher resolution to make detailed regional comparisons, at a haplogroup level, it may be instructive to note the

similarity of percentages across ethno-linguistic groups. For example, H occurs at between one-quarter and one-third of the population of Armenians (30%), Azerbaijanis (29%), Iranian Azeris (25%), Nogais (22%), and Adyghei (30%); Georgians (17%) and Karachays (14%) have slightly lower frequencies (see Ottoni et al. 2011 for Armenian and Azerbaijani; Macaulay et al. 1999 for Adyghei; Tambets et al. 2000 for Georgians; Bermisheva et al. 2004 for Nogais; Asgharzadeh et al. 2011 for Iranian Azeris). Similarly, the precursor to H, haplogroup HV, occurs at 5-10% in most of the same populations, and the same trend holds with haplogroups J, K and T.

The similar frequencies of these mtDNA haplogroups (H, HV, J, K, T, W) across ethno-linguistic boundaries would seem to belie an ancestral Caucasus population having a maternal gene pool consisting of these haplogroups, as well as haplogroup U, which is a more complex matter. While many of these same lineages expanded into Europe, in the Caucasus they show signs of much earlier, pre-LGM diversification (Metspalu et al. 1999: 131-2). Since these haplogroups are all thought to have originated somewhere in Western Asia, and all have coalescence dates well before the LGM (see Achilli et al. 2004 and Roostalu et al. 2007 for H and HV, irrespectively; see Soares et al. 2009 for K; see Metspalu et al. 1999 for T and J; for W see Richards et al. 1998, and our own coalescence estimate), their time depth in the Caucasus may also be quite significant.

IId. Linguistic Diversity in the Caucasus

Questions about language relations and origins loom over any study of population histories in the Caucasus. Although the precise linguistic affiliations of the Azeri and Armenians are still open questions, they are of much less importance to our current concerns than the processes by which the numerous languages categorized as ‘Caucasian’ came to exist relative to their speakers. That there is no definitive answer to the question of whether there was ever one, three, or several proto-Caucasian languages is chief among these concerns.

Attempts on the part of numerous researchers to establish a Caucasian *Sprachbund* based on shared grammatical categories (e.g., ergativity, *suffixaufnahme*, glottalized obstruents and uvular consonants; ჯავახიშვილი 1937; Vogt 1942; Catford 1991; Chirikba 2008) have been largely unsuccessful. Likewise, the proposed union of the Northwest Caucasian, Northeast Caucasian, and Kartvelian language families into a macro-family called Ibero-Caucasian (Чикобава 1955a, 1955b; ჩიქობავა 1948b, 1979) has also fallen out of favor due to the crumbling of its main supporting pillar, namely that that Kartvelian supposedly once had a category of grammatical gender (მნობნო 1978, 1989; Ониани 1985; Chirikba 2008; Tuite 2008). Tuite (1999) has proposed that the Caucasus constitutes a mini-*Sprachbund*, that is, a region of historically interlinked language zones whose languages do not necessarily share a common ancestral language. The advantage of such a view in terms of population histories is its flexibility in permitting a gradual and complex ethnogenesis of Caucasus ethno-linguistic groups.

Grammatical objections aside, it is not entirely impossible for these three language families to share a common linguistic ancestor in very deep history. However, such a scenario would require a greater time depth than implied by archeological evidence of a human presence in the Caucasus. Therefore, recourse to other, more expansive theories of linguistic affiliation and geographic coverage may be necessary. One such hypothesis suggests that Caucasian languages were once spoken not only in Anatolia (see Diakonoff and Starostin 1986 for Hurro-Urartian; Kassian 2010 for Hattic; Oštir 1921 for the Alarodian proposal; see also Kavtaradze 1985, 2002) but even further into the ancient Near Eastern world (see Bobula 1951 and Zakar 1971 for Sumerian affiliations).⁵⁸ Their current geographic distributions would therefore be attributable to migrations or other, more piecemeal demographic reorganizations. Such a scenario both relieves us of the expectation of firmer lexical interrelationships between the languages, and the need to explain the presence (and absence) of loan words from other, older Near Eastern languages. Yet, many historians and archaeologists (e.g., ჯავახიშვილი 1998) have insisted, for example, that Proto-Kartvelian, the ancestor of Georgian and its sister languages, was spoken in an area centered on present-day Georgia.

It cannot be discounted that languages spoken in the northwest and northeast Caucasus, and in Georgia, have their roots in, or are creolized forms of, languages

⁵⁸ Such affiliations are purely lexical as the amount of shared vocabulary between Sumerian and Kartvelian languages is miniscule, and highly problematic, as it cannot be reconstructed beyond the Georgian-Zan level (c. 2500 BCE) (see Klimov 1998; Sahala 2009: 3).

spoken there even before what might be termed the ‘arrival’ of Caucasian languages.⁵⁹

It is well known, albeit understudied philologically or comparatively, that archaic autochthonous words, some for very basic vocabulary, and other lexical features (Климов 1964; see also Дзидзария 1989 for Abkhaz; Tuite 1997, 1999 for Svan), were adopted from pre- or otherwise non-Caucasian languages, and survive in the languages of all three Caucasian families. What we know about these words and forms is less suggestive of a common source for all three of the language families, and more supportive of their gradual arrival and entrenchment, and subsequent areal diffusion. The archaeological and biological data reviewed in this chapter would indicate the direction of this arrival to have been largely from the south and southwest, though Iran cannot be ruled out as the source of certain elements.⁶⁰

⁵⁹ The presence of pre-Indo-European words and lexical forms in Indo-European, for example, is well attested (see e.g., Beekes 2000 and 2010: xiii-xlii; Masica 1979; Matasović 2009: 441), and interpreted as evidence of contact with spoken languages now no longer extant.

⁶⁰ Linguistic studies of pan-Eurasian language families and the isolates wedged between them, while numerous and long-standing (see Bomhard 2008; Dolgopolsky 1998; Greenberg 2005; Ruhlen 1994; Starostin 1989), have yet to reveal indisputable evidence of affinity between them all (e.g., Ringe 1995). Proposed relationships between Caucasian languages and languages spoken in regions beyond Anatolia and Mesopotamia (e.g., Colarusso 1997; Tuite 2006) also have their merits. The most lingering of these is the Basque-Caucasian Hypothesis, a idea initially proposed by Uhlenbeck (1924), and followed up by a number of compelling but ultimately inconclusive studies (e.g., Bouda 1949; Dumézil 1933a, 1933b, 1937; Karst 1931; Lafon 1951; Map 1920; Map 1920; Ruhlen 1994). Study after study of gene frequencies among participating Caucasus populations and Basques has concluded that while they tend to fall at extreme ends of the European range, overall they do not bear any special evolutionary relationship. Findings by Comas et al. (2000) concur with those of Bertorelle et al. (1995), which indicate that Basques and Georgians are at extreme ends ‘of the distribution of several mtDNA haplogroups in Europe/West Asia (high H and V frequencies in Basques, high T frequency in Georgians)’. However, a comparison of Adygei mtDNA data from Macaulay et al. (1999), Armenian mtDNA from Tambets et al. (2000), and the mtDNA haplogroup distribution among Basques from northern Navarre (Cardoso et al. 2011: Table 1) reveals a notable similarity, in that mtDNA haplogroups H, J, K, T, U4, and U5 are shared by these populations, in not dissimilar percentages, and W is also shared by Adygei and Navarre Basque, but was not present not in the sampled Armenian populations. This, coupled with the presence of H, HV, and pre-HV in Armenian populations, the low frequency of HV and total absence of pre-HV among Basques in multiple studies (e.g., Alfonso-Sanchez et al. 2008; Behar et al. 2012; Cardoso et al. 2011; Torroni et al. 2001 did, however, find significant HV in their samples) casts an interesting light upon the Franco-Cantabrian refugium theory (Behar et al. 2012; Cardoso et al. 2011; Lopez-Parra et al. 2009). A Y-

The putative linguistic connections between Kartvelian and other pre-Turkic Anatolian languages are probably the most compelling in this regard. Although the over 300 Kartvelian-Greek words and lexical forms found in common by Furnée (1972, 1979, 1982, 1986; see also გორდეზიანი 1985) are probably closer to twenty (Гамкрелидзе and Иванов 1984: 904-906), the implications for deep and long-lasting proximity of these languages even into relatively recent times is still worth noting, in spite of potential criticism.⁶¹ Gordeziani (1978) has also noted similarities between various Kartvelian and Northern Mediterranean toponymic infixes and suffixes, such as -s(s), -nth- and -nd-.

Notwithstanding the opinion of Gamkrelidze and Ivanov (1985) that proto-Kartvelian and proto-Indo-European demonstrate deep lexical and other structural similarities, the fact of Kartvelian-Greek affinities is significant for a number of reasons. First, the Kartvelian loan words seem to occur evenly throughout historically Greek-speaking regions, from the Balkans to western Anatolian to the communities of the Pontus, suggesting the loaning occurred there rather than through circum-Black Sea back-migration or contact along the Phasis. The even distribution of Greek lexical forms in Georgian also seems to be the case, and thus Hellenic contacts in Colchis can be ruled out as their origin.

chromosome comparison of Biscay Basques, Gipuzkoa Basques (Alonso et al. 2005), Armenians (Nasidze et al. 2003, 2004), and Ossetes (Nasidze et al. 2008) is somewhat less revealing (especially given the lack of subhaplotypes in the Armenian data), but not insignificant given the presences of E and R1b in both Basques and Armenians, and G, J, and K in Basques and Ossetes. Further comparisons are made in Bauchet et al. (2007) and Laayouni et al. (2010).

Barring Colchis, where else but Anatolia could Greek- and Kartvelian-speakers have been in proximity such that aerial diffusion of lexical terms could occur? The fact that Balkan Greek contains Kartvelian loan words is enough to suggest contact in western Anatolia,⁶² if not in the Balkan Peninsula itself. In addition, numerous mythological tales coming down to us as Greek specifically reference the Caucasus. These include the eleventh labor of Hercules, the journey of the Argo, and the resemblance of Prometheus and Amirani (and other North and South Caucasian cognates of this myth). All of these references give credence to some kind of pre-Homeric contact (Braund 1994: 28-9).

Various efforts to date the divergence of the three Caucasian language families have been offered. Again, the most compelling work has been done with Kartvelian, both in terms of temporal framework (Deeters 1930; Климов 1964; Klimov 1994) and the generation of an acceptable family tree (Tuite 1997: 4). The reconstructed Proto-Kartvelian lexicon includes multiple terms for trees (birch, elder, elm, hornbeam), plants (strawberry, whortleberry, *Rhododendron flavum*, *Rhododendron ponticum*) and animals (bear; male and female mountain-goat), which are consistent with a localization in the upland regions of Georgia—especially western Georgia—and eastern Anatolia (Tuite pers. comm.). The agricultural vocabulary is also consistent with a Bronze Age economy, including terms for secondary products such as ‘wool’, ‘weave’, ‘spin’, ‘milk’, but very few names of domestic animals (‘dog’ and ‘goat’ are the best candidates) (Klimov 1998). Also of potential relevance are toponyms in western

⁶² Connection with Pelasgians (a term considered obsolete by Beekes) and perhaps other pre-Greek peoples of Anatolia should not be discounted.

Georgia that indicate the wider range of Svan in the past (notably in the provinces of Mingrelia, Upper Imereti, and Racha-Lechkhumi; Chumburidze et al. 2007: 34).

Some researchers have further detected what they interpret to be evidence of a Northwest Caucasian (Abkhaz-Adyghean) substrate in Mingrelian. Of particular interest are river names which appear to contain the West Caucasian suffixes -ps-/-pš-, meaning ‘water, river’ and -q’va ‘valley’, and are found as far south as Guria (Supsa) and Ach’aria (Ač’q’va) (ჯანდუშია 1940; Чикобава 1948a). Should these West Caucasian traces precede the Kartvelian presence along the eastern coast of the Black Sea, then this would support the hypothesis that Kartvelian diffused into present-day Georgia from the south or southwest. The connection between Kartvelian-speakers and metalworking has been noted in connection with numerous classical authors, including Homer, Herodotus and Strabo, all of whom mention a place called Χαλυβει and its people, variously called Χαλυβεις or Αλιζωνεις who lived along the Phasis and in northeastern Anatolia (Brixhe and Drew-Bear 1982: 74-5), who were well known for their metalworking (Homer II: 856-57; Strabo XII: 22). Proximate tribes also thought to be Kartvelian-speaking include the Μοσσύνοικοι (an ethno/toponym allegedly related to various other names and places, such as Meskheti, a historical region of southern Georgia, Muški, and even more possibly to the Meshech of Genesis 10:2 and 1 Chronicles 1:5).

The gradual moving or pushing eastward of Kartvelian-speakers, as well as putatively Northeast Caucasian-speakers (Иванов 1983; Orel and Starostin 1989), or some element of them, into the Caucasus may well have begun during the Metal Age,

given the geographically neat divisions of the four extant Kartvelian languages, Georgian, Mingrelian, Svan, and Laz. This dynamic possibly even pushed Vainakh and other Northeast Caucasian-speakers into the highlands (Nichols 2004; Tuite 1996). It may be that Persian suzerainty was a driving force in the consolidation of these languages as separate entities. We predict continued historical-linguistic analysis of this family will confirm evidence of a split between Svan and Georgian (or from proto-Kartvelian) in prehistory, perhaps during the 2nd millennium BCE (Deeters 1930; Климов 1994) or even the 3rd millennium (see Nichols 1998), with the split of Mingrelian-Laz and Georgian occurring more recently (Boeder 2005: 6-7; Harris 1991: 10-12).⁶³

The contentious relationship between Kartvelian and the languages of the North Caucasus is no closer to resolution than it was twenty-five years ago. Balanovsky et al.'s (2011) estimation that the split of Northeast Caucasian (Nakh-Daghestan) languages from those of the Northwest (Abkhaz-Adyghean) occurred over 6,000 years ago is based on the assumption that these families form a single North Caucasian superfamily. However, no one has convincingly shown these languages to be related to each other, to Kartvelian, or to any other language family (Comrie 2005). In fact, the linguistic data would seem to support the opposite viewpoint.

⁶³ 'Laz', as Michael Meeker (1971: 320-21) points out, is not always synonymous with the Laz or Lazi, who are Kartvelian-speakers in Anatolia, but is instead a general and evidently very old term for non-Turkish eastern shore Black Sea peoples. This usage of 'Laz' is evidently an exonym, whereas the reference to Laz as a Kartvelian-speaking minority in Anatolia is an endonym. However divergent and complex their usages, and for whatever reasons, the co-validity of these terms indicates an ancient presence of Kartvelian-speakers in eastern Anatolia. A broader-spectrum study of Kartvelian affinities with the other pre-Turkic languages of Anatolia (e.g., Luwian, Hittite, Mittani, Armenian, and Urartian) will continue to contribute to our understanding of this matter.

More convincing perhaps is the assessment of splits within the Northeast Caucasian family, namely Nakh from Daghestan, as occurring some 5,000 years ago. These splits did not necessarily happen *in situ*, nor can they account for cases of recent areal diffusion, an example of which might be the ergative suffix -em in Svan, which has been considered by some scholars to be a borrowing from Circassian (see Топурия 2002.)⁶⁴ Although the correlation between such high frequencies of Y-chromosome haplogroups J1 and J2 (as well as novel subgroups, which are common in the North Caucasus) and both geography and language is indicative of long-term habitation, we cannot dismiss out of hand a possible relationship between these lineages and Urartian expansions, or post-Urartian Nakh retreats to the hinterlands (Akurgal 2001; Bryce 2005; Piotrovsky 1967, 1969), as well as a possible Hurrian substratum in the Northeast Caucasian languages and Urartian (Diakonov 1971, 1981a, 1981b). Other researchers cite the Koban culture (1100-400 BCE) as the common substrate for many present-day North Caucasian-speaking peoples (e.g., Козенкова 1977, 1979, 1989, 1990, 1998; Мелюкова 1989). Given the depth of the relationship between language and genes, as explicated by Balanovsky et al. (2011), we can dismiss any proposed connection to Arab imperial expansion in the 8th century CE.

Should the Kartvelian historical language trajectory indeed reach deep into Anatolia, as do some of the Indo-European languages of antiquity, their routes of expansion may have followed the Black Sea coast rather than the Ararat Plain, given

⁶⁴ An in-depth discussion of the relationships between the three Caucasian families, while interesting, is far too complex and multi-directional to suit the present discussion. For an overview of this topic, see Boeder (2005), Comrie (2005), Hewitt (2005, 2006), and Tuite (1999).

there is no significant presence of Kartvelian-speaking peoples south of modern day Georgia. However, this may not always have been the case. In the late 3rd millennium BCE, settlements of the Kura-Araxes culture began to be replaced by those of the early Trialeti culture, which exhibits cultural ties with the highly developed cultures of the ancient world, particularly those from the Aegean (Gimbutas 1965: 92-3). Of these cultural practices, the most famous are the tumulus or kurgan burials in which evidently elite members of society were buried, sometimes with abundant gold and even four-wheeled carts (Kushnareva 1997: 108). Kurgan burials and wheeled carts are routinely associated with Indo-European culture, and therefore the Trialeti Culture may indeed have been an Indo-European-speaking phenomenon, at least among elites, or a mix of Indo-European- and Kartvelian-speakers (e.g., Burney 1958; see Джапаридзе 1960: 18 for speculation on the connection between these carts and those of the Near East).

The final centuries of the ancient Near East were complex, and made even more so by the presence of pockets of Turkic-speaking populations (for Karachays, see Мизиев 1994; for Кумыкs, see Гаджиева 1961). The subject of Turkmen in the history of the Caucasus is rarely dealt with. It has been suggested that these and other Turkic groups gradually diffused from the Russian steppe into the North Caucasus (and perhaps to some degree from Persia to the south), and both mixed with and forced some of the North Caucasian-speaking peoples to move into the high mountains (Абрамова 1989; Мелюкова 1989; see also Pritsak 1967 for Golden Horde connections). It has further been suggested that the defeat of the Alans by the Mongols and subsequent conquest by Tamerlane in the 14th century CE may have precipitated a re-expansion of

indigenous inhabitants into former Alan lands (Alemany 2000; Федеров 1983).

Moreover, the relations of these Turkic peoples to the earlier arriving Nogai people remain unclear (Кочекаев 1988). In spite of this great complexity, we may perhaps be able to make some sense of the overall directions of influx and thereby the genetic heritage of the Neolithic populations.

Over the years, numerous claims have been made about the concomitance of early Neolithic farmers (as well as pre-Neolithic population) and the spread of Indo-European languages (e.g., Cavalli-Sforza et al. 1994; Menozzi et al. 1978; Sokal et al. 1991). Some of these claims have been controversial (e.g., Гамкрелидзе and Иванов 1984, 1995). Whatever the case in Europe, where Indo-European languages constitute a near total monopoly (Uralic languages such as Finnish, Hungarian and Estonian being the only notable exceptions, in addition to the isolate Basque), with the exception of Armenian and Ossetian (whose presence has established historical dimensions), these languages are essentially non-existent in the Caucasus. Within the current political boundaries of the Caucasus region, northern dialects of Kurdish are spoken in Kurmanji villages in all three South Caucasian countries (Spät 2005), and Russian is spoken as a matter of recent historical course. Similarly, the presence of Armenian and Ossetian cannot be associated with the farming/language dispersal hypothesis.⁶⁵

⁶⁵ Neolithic farmers and pre-Neolithic populations are said to have swept (or otherwise diffused) across western Eurasia, taking early Indo-European variations with them as they assimilated or otherwise eliminated the presence of previous Epipaleolithic and Paleolithic language everywhere but in Basque country and in the highland Caucasus. If indeed this is the case in the South Caucasus, there should be an indigenous Indo-European language in the Caucasus other than Armenian and Ossetian. This fact alone interferes with the simplicity of the farming/Indo-European dispersal hypothesis (Bellwood and Renfrew 2002; Zvelebil and Zvelebil 1988).

IIe. Summary

The regional uniqueness of Caucasus languages has long influenced thinking that the populations of the region represent an autochthonous and highly archaic population. Our review of archaeological, genetic, and linguistic lines of evidence indicates this might be partially true. Since many key topics have yet to be fully explored, we cannot yet be certain about timing and directionality of settlement in the Caucasus, or in what ways these timings and processes mirrored or otherwise affected Paleolithic and Neolithic settlement processes in other parts of Eurasia, specifically Europe. However, the dearth of Paleolithic materials from Anatolia makes it difficult to confirm the time-depth and extent of the Levant-Caucasus trajectory.

The Levantine-Anatolia-Caucasus trend continues into the Neolithic, with food producing sites appearing initially in the western and southern parts of the South Caucasus, and also with material cultural affinities to the Levant. The Levantine-Anatolia-Caucasus trajectory is corroborated by numerous studies of genetic diversity in these regions, which indicate male-mediated late Mesolithic and early Neolithic migrations to the Caucasus via the Anatolian highlands. The mtDNA story is far more complex and possibly reflects in large part the presence of lineages dating to the Upper Paleolithic, as is the case in Europe, as well as others brought by later settlers.

Notwithstanding the ethno-linguistic ‘zone’ patterning in the North Caucasus (Balanovsky et al. 2011), which likely tells us less about the genes carried by initial settlers and more about social behaviors since these settlements, the autosomal IBD

patterns favor a Near Eastern origin for all Caucasus populations except for those established during the Turkic khanates. Refined demographic patterning can be seen in language family association. Coalescence analysis of North Caucasus languages, in parallel with estimates for Y-chromosome haplogroups, indicates that these languages are older, in situ, than Kartvelian in the South (Balanovsky et al. 2011; Figure S2). Whether this pattern is attributable to population pressures from the south or to less perceptible processes is not yet known.

The relationship between the Carpatho-Balkan Metallurgical Province, Maikop, and the phenomenon of later kurgan cultures is also not yet well understood. However, it does suggest social change, if not the arrival of new populations, in the region. In fact, with the exception of certain well known, and in some case well-documented, historical events, i.e., Azeris, Ossetes, and the Turkic languages of the North Caucasus, there is very little reason to believe that any major shift in allele/haplogroup frequencies has occurred in the Caucasus since at least this time, if not well before. However much the vicissitudes of empires in the Caucasus between Antiquity and the early modern periods may have affected the demographics of language and social custom, there is also little evidence for major settlement projects during these periods. Thus, the cultural diversity of Caucasus populations results from prehistoric settlement events and to socio-cultural shifts both old and new.

CHAPTER III: METHODS

Given the sparseness of historical and archaeological materials particular to Svaneti, this study relies mainly on genetic data to delineate the origin and prehistory of Svans. This section outlines the molecular and quantitative methods utilized for this purpose, beginning with the inception of the study, sample collection, laboratory methods, and quantitative techniques.

III.a. Conception and Funding of the Project

In the summer of 2011, I received two small travel stipends, one from the University of Pennsylvania Museum of Anthropology and Archaeology and another from the Penn Anthropology Department, to travel abroad for the purpose of establishing necessary contacts and credentials to perform dissertation-related fieldwork. Originally, it was my intention to study the genetic history of the Urum population, an ethnically Greek but Turkic-speaking group living in southern Georgia. Upon arrival, I contacted old friends from my days doing archaeology at the Vani site, and they in turn connected me to Dr. Goderdzi Narimanishvili (an archaeologist working in Samtskhe-Javakheti). He ultimately directed me to Dr. Lia Bitadze, a senior researcher at the Laboratory of Anthropological Research, and Head of the Department of Anthropology at the Ivane Javakhishvili Institute of History and Ethnology, Tbilisi State University. She and I discussed our mutual research interests. Joining us in subsequent meetings were Dr. Ramaz Shengelia, Professor of medicine at Tbilisi State Medical Institute, and Dr. David Chitanava, a researcher at Dr. Bitadze's Laboratory of

Anthropological Studies, and a specialist in Georgian prehistory and history. It soon became evident through our conversations that my original idea to study the origins of the Urums was infeasible without extensive travel to southern Russia (as many members of this ethnic group had emigrated in recent years), and that a country-wide study of Georgians and minority populations in Georgia was possible with this group of researchers.

Based on this agreed upon approach to investigating Georgian history, over the course of the next year, my advisor, Dr. Theodore Schurr, and I prepared grant applications to support the project and submitted a research protocol to the Penn IRB #8. In August 2012, we were awarded an NSF EAGER grant (BCS-1249281) for the research to be conducted in Svaneti. The Penn IRB #8 also approved the research protocol (#814693) during the same month (**Appendices 1 and 2**). We also worked with Dr. Shengelia to obtain permission to perform scientific work in Georgia from the Georgian Committee for Bioethics, and were successful in doing so due in large part to Dr. Shengelia's efforts.

III.b. Sample Collection and DNA Isolation

In August of 2012, we returned to Georgia and conducted ethnographic fieldwork in village districts and townlets throughout Upper Svaneti (see map). During this month, we enrolled in the study a total of 184 non-consanguineous Svan adults from Mestia, Laghami, Mulakhi, Kala, Ipari, Ushguli, Tskhumari, Becho, Etseri, Latali, Chuberi, Khaishi, and Idliani. In addition, sixteen unrelated non-Svan Georgians from

Tbilisi also provided samples, bringing the total number of participants to 200, of whom 103 were men.

Written informed consent was obtained with Georgian-language consent forms (**Appendix 2**; see **Appendix 3** for English translation) prior to the collection of buccal swabs and genealogical information (**Appendix 4**; see **Appendix 5** for English translation) from each participant. Participants identified their age and birthplace, their parents' names, ethnicity, and birthplaces (when known), and their four grandparents' names, ethnicity, and birthplace (also when known). Although all unrelated males and females were encouraged to participate, when working with men, emphasis was placed on obtaining samples from individuals representing as many different Svan surnames (i.e., clan-affiliated lineages) as possible, and from as many of the Svan settlements as possible. All sampling and consent procedures were carried out with permission of the University of Pennsylvania IRB #8 (protocol #814693) and the Georgian Committee on Bioethics.

III.c. Molecular Genetic Analysis

Upon completion of fieldwork, I brought the samples back to the Laboratory of Molecular Anthropology at Penn (LMAP) for DNA extraction and analysis. I extracted the genomic DNA from the buccal swab samples using Puregene Blood Core B kits (Qiagen), using a slightly modified version of the manufacturer's protocol. The mtDNA analysis was conducted by Penn undergrads Andrew Azzam and Kristi Edleson, high school intern Victoria Groner, and Dr. Schurr, using published methods

described below. Y-chromosomes were analyzed using SNP and short tandem repeat (STR) loci by Penn undergrad Akiva Sanders, post-doctoral fellow Dr. Miguel Vilar, and Dr. Schurr, using published methods described below.

III.c.1. mtDNA Analysis

For all 200 samples, the entire mtDNA control region (CR) was sequenced using published methods (Gaietski et al. 2011; Schurr et al. 2012; Zhadanov et al. 2010).

These samples were screened for a set of single nucleotide polymorphisms (SNPs) in the coding region of the mtDNA that define the basal structure of the mtDNA phylogeny, and then others defining specific haplogroups and their sub-branches, using custom ABI TaqMan® assays (Gaietski et al. 2011; Schurr et al. 2012; Zhadanov et al. 2010). Overall, this analysis provided high-resolution mtDNA data for the Svan population. All polymorphic nucleotides were defined relative to the revised Cambridge reference sequence (rCRS). The combination of SNP data and CR sequences defined maternal haplotypes in these individuals, and all haplogroups were ascertained relative to mtDNA databases (e.g., Phylotree; van Oven and Kayser 2009).

III.c.2. Y-chromosome Analysis

To identify paternal haplotypes, we surveyed phylogenetically informative SNPs in the non-recombining region of the Y-chromosome (NRY) (Cruciani et al. 2011; Francalacci et al. 2013; Karafet et al. 2008). The Y-chromosome of each male participant was characterized using several methods. Most of the SNPs and fragment length polymorphisms were characterized using custom ABI TaqMan® assays (Applied

Biosystems) (Gaiieski et al. 2011; Schurr et al. 2012; Zhadanov et al. 2010). The SNPs included (MI68, M89, M45, M9, M201, P15, M304, M69, MI70, M207, M96, LLY22), with these markers being characterized using custom TaqMan assays read on an ABI Prism® 7900 HT Real-Time PCR System. Paternal haplotypes were further defined through the analysis of male samples with 17 Y-STRs in the ABI AmpF ℓ STR Y-filer® PCR Amplification Kit, as previously described (Zhadanov et al. 2010; Gaiieski et al. 2011; Schurr et al. 2012). A separate multiplex reaction was used to characterize six additional fragment length polymorphisms (M17, M60, M91, M139, M175, M186) and two additional Y-STRs (DYS388, DYS426) (Zhadanov et al. 2010; Gaiieski et al. 2011; Schurr et al. 2012). These markers were read on a 3130xl Genetic Analyzer with GeneMapper ID v3.2 software. The assignment of each male sample to a NRY haplogroup followed the conventions outlined by the Y Chromosome Consortium (2002) and Karafet et al. (2008). The combination of SNPs and STR alleles defined paternal lineages and haplotypes, respectively, for each male individual.

III.d. Genetic Data Analysis

III.d.1. Descriptive Statistics

We estimated the basic descriptive statistics for the mtDNA and Y-chromosome data using Arlequin v3.11 (Excoffier and Lischer 2010). These statistics included the nucleotide diversity, gene diversity, haplotype sharing and pairwise mismatch analysis for mtDNA sequences, and also gene diversity for the Y-STR haplotypes. In addition, Tajima's D (Tajima and Nei 1984) and Fu's F_s (Fu 1997) were calculated from mtDNA

sequences to assess the possible influence of selection on genetic variation, using Arlequin.

To assess the degree of regional differentiation in the Caucasus and the greater Near East, we performed analyses of molecular variation (AMOVA) based on haplogroup and haplotypic frequencies for both mtDNA and NRY data sets. AMOVA is a statistical platform designed to measure the partitioning of variance at different levels of population subdivision, giving rise to an analogue of Phi-statistics called F-statistics (Excoffier and Lischer 2010). This analysis partitioned the total variance among haplogroup and haplotypic frequencies in Svans and comparative populations into covariance components based on intra-individual differences, inter-individual differences, and/or inter-population differences (Excoffier et al. 2005).

III.d.2. Population Subdivision

To better understand Svan genetic ancestry, we compared our data with those from other Eurasian populations (e.g., Levantine and Peninsular Arab, Iranian, Anatolian, and Eastern European). For the mtDNA data, F_{ST} values were estimated for the Svans and comparative populations using HVS-I sequences and relative haplogroup frequencies with Arlequin v.3.5.1.2 (Excoffier et al. 2005). For the Y-chromosome data, pairwise F_{ST} and R_{ST} genetic distances between the Svan villages, and between Svans and comparative populations, were estimated using 17 Y-chromosome STR (Y-STR) haplotypes (DYS19, 385I, 385II, 389I, 389II, 390, 391, 392, 393, 437, 438, 439 and 448; we excluded DYS388 and DYS426 for reasons of commensurability with

other data sets) and NRY haplogroup frequencies. The F_{ST} and R_{ST} estimates from these analyses were visualized using multidimensional scaling (MDS) with R version 3.1.2, with the help of Dr. Eugene Potapov of Bryn Athyn College. **Figure 13** was generated with SPSS version 22.0.0.0 with the help of Dr. Miguel Vilar. These analyses provided insights into the genetic relationships between Svans and geographically proximate populations, as well as their genetic affinities with comparative various regional populations.

III.d.3. Demographic Analysis

The Svan mtDNA and NRY haplotypes were sorted by the home village of the participants to look for local patterns of genetic differentiation. For the mtDNA data sorting, participants reported belonging to fourteen separate village districts. Home villages reported less than three times were regarded as statistically insignificant and left out of the analysis, as were reported home villages outside Svaneti or Abkhazia. In one case, a reported home village (ჯამუში [Jamushi]) could not be geographically verified in either Svaneti or Abkhazia, and therefore was also left out (thus reducing the total sample set by ten, inclusive of the eight mentioned below). For the NRY data, male participants reported coming from ten different village districts. As noted above, home villages reported less than three times were regarded as statistically insignificant and left out of the analysis, as were reported home villages outside Svaneti or Abkhazia (thus reducing the total sample set by eight). These subtractions reduced the total number of individuals for these analyses to 174 women and 77 men, respectively. Data

sorted in this fashion were then analyzed for pairwise F_{ST} values and population differentiation.

IIIId.4. Phylogenetic Analysis

To elucidate the phylogenetic history of genetic lineages present in Svaneti and between Svaneti and the greater Near East, as well as the ages of these haplogroups through coalescence estimation, we used network analysis with both mtDNA and NRY data sets, using NETWORK 4.6.1.3 (Bandelt et al. 1999). Such networks reveal phylogenetic or genealogical connections among haplotypes, irrespective of whether they are shared across a language family or geographic grouping.

For the mtDNA data, median-joining networks were constructed for haplogroups W and X. These two haplogroups were chosen based on their unusually high frequencies in the Svans. We based our mutation-weighting scheme on that described in Bandelt et al. (2002), in which fast-evolving sites were given lower weights relative to other less mutable sites. For the most recent common ancestor (TMRCA) estimates for haplogroups, a mutation rate of one mutation per 16,667 years was used for HVS-I [np 16024-16383] (Soares et al. 2009).

We also inferred patterns of diversity and estimated coalescence times for Y-chromosome haplotypes with NETWORK 4.6.1.3 (Bandelt et al. 1999). Median-joining networks based on 17 Y-STR haplotypes were created for haplogroups G2a, R1a, and I2a, these being the most commonly occurring paternal haplogroups among Svan males. To make TMRCA estimates, we calculated ρ -statistics with the Y-STR

data, with the founder haplotype being inferred as the one most central to the network (Sengupta et al. 2006; Dulik et al. 2011, 2012a). We used both a pedigree-based mutation rate (one mutation per 453 years, estimated by taking the inverse per generation mutation rate of each locus used multiplied by the number of loci and by a generation time of 25 years; Chandler 2006; Vilar et al. 2014), and an evolutionary mutation rate of 2778 years.⁶⁶ All networks were visualized using Network Publisher v1.2.0.0 (Fluxus Technology Ltd).

III.e. Comparative Data

To elucidate the genetic affinities of Svans, we compared their mtDNA and Y-chromosome data to those of populations from the Caucasus and Middle East. The mtDNA data were drawn from Abkhazians, Armenians, Circassians, Georgians, Kabardians, North Ossetians and South Ossetians (Nasidze et al. 2004); Anatolians (Gökçümen et al. 2011) and Iranians (Terreros et al. 2011). This analysis was conducted on the basis of the relative frequencies of haplogroups C, D, H, I1a, I1c, J, K, M, R0a1a, T*, T1, T2, U*, U1, U2, U3, U4, U5, U5a, U6, U7, W*, W6, X2*, X2a, and X4. For Georgians we used unpublished data reported in summary form by Nasidze et al. (2004). This was obtained from his former colleague Dr. Mark Stoneking from the Institute of Evolutionary Anthropology in Leipzig, Germany.⁶⁷

⁶⁶ In their paper on G2a, Rootsi et al. (2012) used an evolutionary effective mutation rate of 6.910^{-4} . We converted this figure for Network using on the basis of 25 years per 0.000691 mutations = x years per 1 mutation, such that $x = 25/0.000691$.

⁶⁷ Fragment lengths for the analysis of mtDNA hypervariable regions were as follows: Nasidze et al. 2004: 16024 to 16400; Gökçümen et al. 2011: 16000 to 16400; Terreros et al. 2011: 16019 to 16569.

The comparative NRY data were drawn from Abkhaz, Circassians, and North Ossetians (Balanovsky et al. 2011), Anatolians (Gökçümen et al. 2011), and Armenians (Herrera et al. 2011). This analysis was conducted on the basis of the relative proportions of NRY haplogroups (which were primarily G2ala, G2alc, R1a, I2a, J2alb, J1, and R1b). Data for Kabardine and South Ossetian populations were left out of the analysis due to the low number of Y-STR markers used in the source publication (Nasidze et al. 2004). Unfortunately, we were unable to find appropriate published data for Iranian populations. Email notes sent to Viola Grugni, lead author of the Grugni et al. (2012) study on Iranian genetic diversity, to obtain such information were unanswered. Furthermore, when reporting their Armenian NRY data, Herrera et al. (2011) did not indicate sample sizes for the observed Y-STR haplotypes, thus forcing us to assume, however improbable, that all such haplotypes appeared only once in these Armenians. Emails requesting the frequency information from Dr. Herrera went unanswered.

Overall, we used 16024-16383 as the set length of HVS-I used for all samples analyzed in this dissertation.

CHAPTER IV: RESULTS

IV.a. mtDNA Diversity in Svans

IV.a.1. Haplogroup and Haplotype Diversity

As seen in **Figure 12**, the Svans exhibited a diverse array of mtDNA lineages, with the majority being of putative West Eurasian or North African origin. Of the 11 distinct maternal lineages present in the Svans, haplogroups H (18%), K (16%), X2 (11%) and W6 (11%) together accounted for nearly half of them. The next most common but still relatively low frequency (i.e., <10%) haplogroups included U1 (8%), U2 (6%) and T2 (5%). The diversity of haplogroup U in the Svans is remarkable, inasmuch as seven of the nine major U haplogroups are present. Several other haplogroups with broadly Near Eastern points of origin were also present at low percentages (e.g., M1, R0a1, N1b1, T), while East Eurasian haplogroups C and D accounted for 6% of the total. One noteworthy finding was the high frequency of haplogroup W6 mtDNAs in the Svans, which at 11% was the highest percentage ever seen in a single population.

Our characterization of mtDNA CR sequences from 200 participants yielded 115 distinct mtDNA haplotypes. The data for CR sequences encompassing np 16024-16569, inclusive of the HVS-I (np 16024-16383), are reported in **Appendix 6**. Of the 200 participants, 184 self-identified as Svans and the other 16 as non-Svan Georgians. In those who identified as Svans, we detected 83 distinct HVS-I haplotypes, whereas we found seven haplotypes exclusive to Georgians. Svans and Georgians shared only eight HVS-I haplotypes (occurring in H, K, U2, U3, U5, W6), suggesting considerable

divergence (and modest gene flow) between them (**Appendix 6**). mtDNA haplogroups otherwise shared by Svans and Georgians included C, J, T1, U1, U2 and U7. Taken together, there are almost as many different haplogroups shared between these populations as there were Georgians in the sample base, and there are no mtDNA haplogroups which appear exclusively in Georgians (though T1 included only one Svan individual). These facts point to moderate divergence between Svans and Georgians in terms of maternal lineages, but a broader set of Georgians is needed for a more precise comparison.

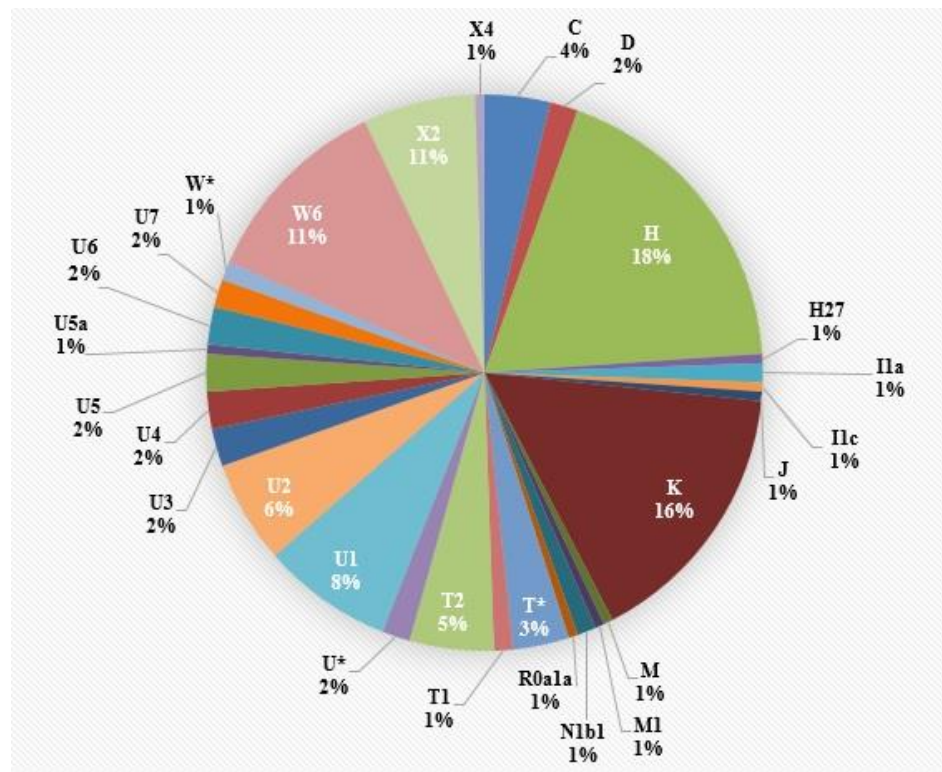


Figure 12. Svan mtDNA haplogroup frequencies

IV.a.2. Descriptive Statistics

We analyzed mtDNA sequence diversity in Svans and comparative populations using a number of descriptive statistics (**Table 2**). The Svans were relatively similar in their HVS-I sequence diversity to the comparative populations, which in itself suggested very little. However, gene diversity (i.e., the probability that two randomly chosen haplotypes are different) in all populations was fairly high, with most values approaching 1 (meaning they are highly diverse), while nucleotide diversity values (i.e., the probability that two randomly chosen nucleotide sites are different) were relatively similar across all groups. High levels of gene diversity are generally suggestive of either diversity within the source populations, or population differentiation *in situ*.

Mean pairwise differences (i.e., the mean value for the number of mutations by which each pair of haplotypes in the population differ) in Svans were greater than those of Circassians or Kabardians but less than those for Abkhaz and South Ossetians (**Table 2**). Thus, Svans fell between these two groups of populations in terms of relative haplotype diversity. Since the variances of pairwise nucleotide differences are generally greater due to migration than isolation (Wakeley 1996), and since Abkhazia and South Ossetia are situated along traditional routes of human transport, it would seem reasonable that these areas would have a more cosmopolitan character. However, the data in **Table 2** also indicate all these populations to be relatively similar, especially once the standard errors are considered, as well as the fact that the greater sample sizes of Anatolians and South Ossetians could contribute to their overall diversity here.

Population	n	# of haplotypes	Gene diversity	Nucleotide diversity	Mean pairwise differences
Svans	184	103	0.989 ± 0.002	0.029 ± 0.015	5.637 ± 2.717
Abkhaz	27	19	0.969 ± 0.018	0.030 ± 0.016	5.858 ± 2.888
Anatolians	163	104	0.990 ± 0.003	0.027 ± 0.014	5.212 ± 2.535
Armenians	42	36	0.981 ± 0.014	0.027 ± 0.015	5.271 ± 2.598
Circassians	43	39	0.989 ± 0.011	0.024 ± 0.013	4.761 ± 2.374
Georgians	72	55	0.981 ± 0.010	0.029 ± 0.016	5.690 ± 2.759
Iranians	109	94	0.996 ± 0.002	0.036 ± 0.019	7.036 ± 3.330
Kabardians	51	36	0.975 ± 0.011	0.024 ± 0.013	4.762 ± 2.370
N. Ossetians	126	67	0.968 ± 0.009	0.026 ± 0.014	5.035 ± 2.462
S. Ossetians	201	76	0.972 ± 0.005	0.031 ± 0.016	6.062 ± 2.899

Table 2. Descriptive statistics for mtDNA HVS-I haplotypes in Svaneti and comparative populations

IV.a.3. Population Subdivision

To better understand the relationship between Svans and their neighbors in the Caucasus and greater Near East, we generated F_{ST} estimates from HVS-I sequences for Svans and comparative populations (**Table 3**), and visualized them in a MDS plot (**Figure 13**). In this plot, Caucasus populations formed a cluster with relatively even distribution. Though the overall distance between any two populations was not greater than 1.5, the outer triangle formed by the Svans, Abkhaz, and South Ossetians situates them as the populations being the most genetically diverged from other groups. Whether this genetic distance is indicative of a greater time depth (i.e., coupled with processes such as genetic drift, differential reproductive success over time in an isolated community) separating these otherwise geographically proximate populations, or

admixture from different sources outside the region, was not immediately clear. However, the F_{ST} estimate (**Table 3**) for the Svans compared to other populations was not especially elevated, thus indicating the relatively close relationship of Svans with other regional populations, and again, the diversity of the Caucasus, at least as its maternal lineages are concerned. This fact may also be seen in the MDS plot (**Figure 13**) generated from these same F_{ST} estimates. We can also see much differentiation between populations with a few exceptions (e.g., Armenians not differentiated from Iranians, Circassians not dif from Kabardians). The differentiation is all the more notable given the low stress value, which suggests this is a good representation of population distinctions.

We also generated F_{ST} estimates from mtDNA haplogroup frequencies (**Figure 14**) using eight of the ten populations⁶⁸ analyzed in **Figure 13**. In this plot, the North Caucasus populations clustered closely together, with the four South Caucasus populations forming a more diffuse triangle around them. South Ossetians were equidistant between Svans and the North Caucasus populations, which makes sense geographically, and Georgians, while more distant, were also approximately equidistant between the North Caucasus populations. Armenians were an outlier. While this pattern contrasts somewhat with the view of population histories found in the plot generated from mtDNA HVS-I sequences (**Figure 13**), the haplogroup plot would probably not look terribly different were the Anatolians and Iranians to have been included. Nevertheless, the distance between the Svans and Abkhaz in both plots is

⁶⁸ Commensurate data for Iranians and Anatolians was not available.

notable, given their geographic proximity. Although the Svans and Abkhaz are neighbors geographically, they speak languages in different families. Thus, we may be seeing, in the genetic record, evidence of a population transition otherwise lost to historical record.

Pop.	Svan	Abk	Anat	Arm	Circ	Geo	Iran	Kab	NOss	SOss
Svan	0	+	+	+	+	+	+	+	+	+
Abk	0.024	0	+	+	+	+	+	+	+	+
Anat	0.016	0.025	0	+	+	+	+	+	+	+
Arm	0.029	0.041	0.017	0	+	+	-	+	+	+
Circ	0.021	0.034	0.021	0.012	0	-	+	-	+	+
Geo	0.020	0.023	0.01	0.011	0.004	0	+	-	+	+
Iran	0.025	0.021	0.008	0.006	0.018	0.011	0	+	+	+
Kab	0.013	0.016	0.012	0.011	0.001	0.006	0.014	0	+	+
NOss	0.025	0.024	0.014	0.029	0.018	0.018	0.019	0.007	0	+
SOss	0.047	0.044	0.018	0.022	0.041	0.029	0.014	0.034	0.037	0

Table 3. F_{ST} estimates generated from mtDNA HVS-I sequences for Svans and comparative populations. The significance values are shown as pluses (+) and minuses (-), with (+) indicating significant differences at $p = 0.050$.

Population Key: Svan=Svan; Abk=Abkhaz; NOss=North Ossetian; SOss=South Ossetian; Kab=Kabardian; Iran=Iranian; Anat=Anatolian; Arm=Armenian; Circ=Circassian; and Geo=Georgian [Normalized Raw Stress=.03190]

The results of the AMOVA based on F_{ST} estimates for Svans and regional populations (**Table 3**) are shown in **Tables 4** and **5**. The percentage of mtDNA variation among groups⁶⁹ using the pairwise distance method was 2.27 and that within groups⁷⁰ 97.73, respectively. The mtDNA sequence diversity within the groupings of populations is not entirely surprising, given the number of haplogroups shared between in the Svans and their neighbors. This result indicates that 2.27% of the variance between these populations is due to genetic differences between them, with 97.73% of variance reflecting shared genetic variation amongst them.

⁶⁹ i.e., how much of the total variation is due to structured variation within the group itself.

⁷⁰ i.e., how much of the total variation is due to variation between groups being compared.

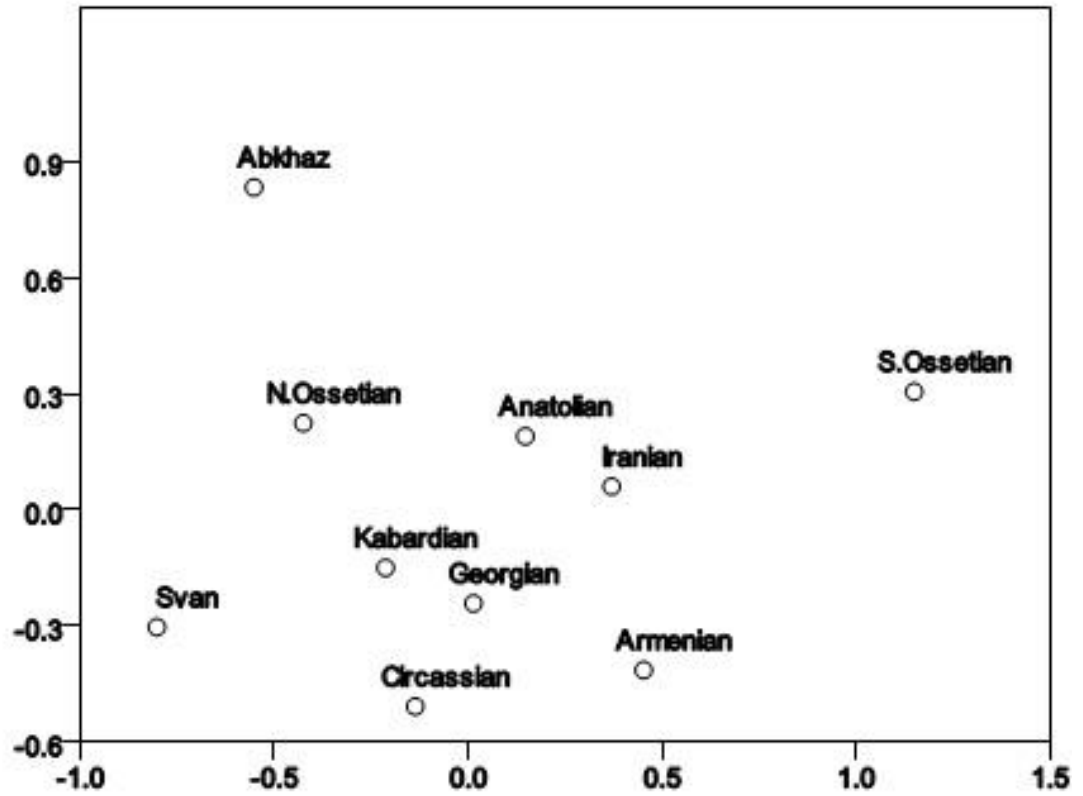


Figure 13. An MDS plot of F_{ST} values estimated using mtDNA HVS-I sequences from Svans and neighboring Caucasus populations

Source of Variation	Sum of Squares	Variance Components	Percentage of Variation
Among Populations	83.087	0.06565	2.27
Within Populations	2841.688	2.82193	97.73
Total	2924.775	2.88758	

Table 4. AMOVA results for mtDNA HVS-I sequences, based on the pairwise distance method

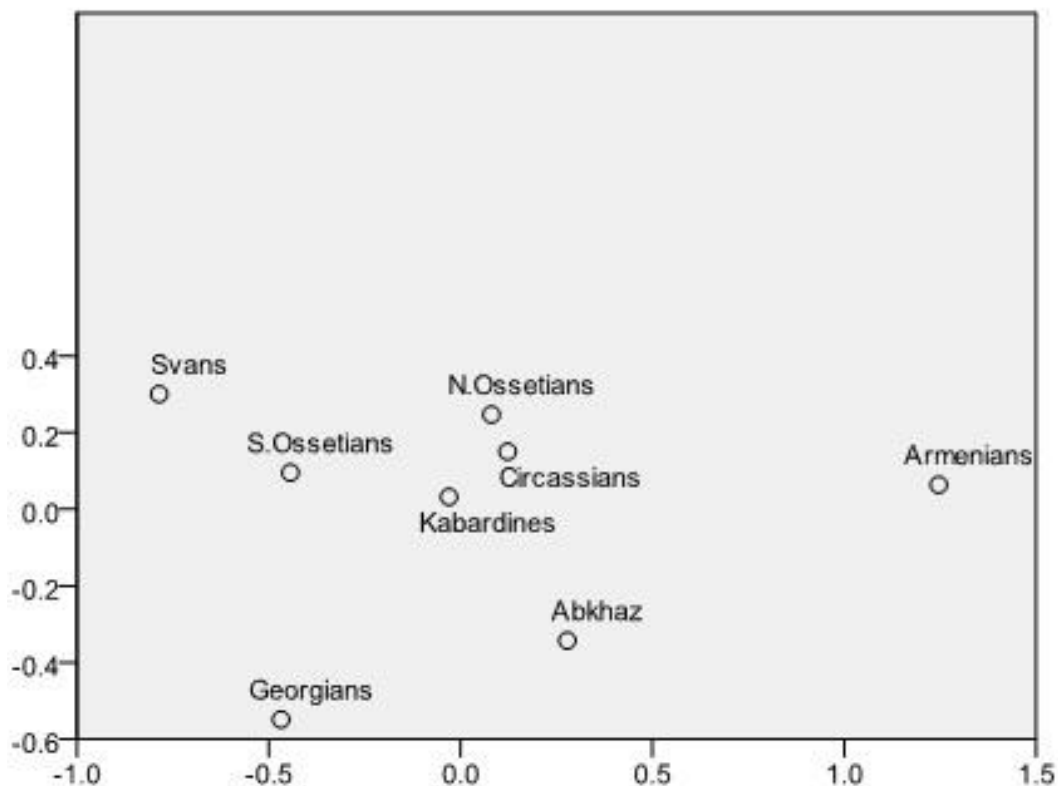


Figure 14. An MDS plot of F_{ST} values estimated using mtDNA haplogroup frequencies from Svans and neighboring Caucasus populations

In **Table 5**, Svans and comparative populations have been separated by their location in (and linguistic affiliation to) the North or South Caucasus and subjected to AMOVA. As seen in **Table 4**, all of the populations seemed to share the vast majority of their haplotype diversity, with only a small proportion arising from mtDNA haplotype differences between them. When we subtracted Iranians and Anatolians from the second AMOVA, the percentage variations changed only slightly (0.11 among groups; 2.34 among populations within groups; and 97.55 within populations). The lack of change helps to confirm that Iranian, Anatolian, and North and South Caucasus share a common set of maternal lineages. These results mean that recourse to

geography is not enough to explain the patterns of mtDNA variation seen in these populations.

Source of Variation	Sum of Squares	Variance Components	Percentage of Variation
Among Groups	14.094	0.01394	0.48
Among Populations within Groups	68.993	0.05973	2.06
Within Populations	2841.688	2.82193	97.46
Total	2924.775	2.89560	

Table 5. AMOVA of F_{ST} values estimated with mtDNA HVS-I haplotype data for Svans and comparative populations (inclusive of North-South Caucasus geographic affinities)

We also analyzed mtDNA haplotype frequencies at the village-level in Svaneti with AMOVA using F_{ST} values estimated from them (**Appendix 7**). Since the distribution of villages in the MDS plot (**Figure 15**) seemed to reflect our sampling process (i.e., disproportionately fewer samples collected from Kala and Ushguli) rather than geography, this analysis did not yield any evidence of long-term differentiation. Significance values for these data were almost entirely negative, with the exception of Kala and Ushguli, whose positive values were likely related to their low sample sizes (2 in Kala; 5 in Ushguli) (**Appendix 7**). The reasons for this finding could possibly be historical, as Svan serfs continued to be bought and sold (and thus moved around) until the late 19th century (or in some cases into the 20th). At the time of abolition, freed peasants were given a small plot of land, on which many families still reside (Авалиани

1913; Гасвиани 1980). If any patterns survived the feudal system itself, the post-abolition demographic reorganization may have muted them entirely. There are two potential exceptions to this history, and they are the landed aristocracy themselves, and the residents of Upper Bal, who are said to have been partially exempt from the feudal system (Авалиани 1913).

	Becho	Chuberi	Etseri	Idliani	Ipari	Kala	Khaishi	Laghami	Latali	Lenjeri	Mestia	Mulakhi	Tshkumari	Ushguli
Becho	0	-	-	-	-	+	-	-	-	-	-	+	-	+
Chuberi	0.043	0	-	-	-	-	-	-	+	-	-	-	-	-
Etseri	0.006	-0.014	0	-	-	+	-	-	-	-	-	-	-	-
Idliani	0.024	0.042	0.009	0	-	+	-	-	-	-	-	-	-	-
Ipari	0.007	0.006	-0.018	-0.011	0	+	-	-	-	-	-	-	-	+
Kala	0.179	0.087	0.120	0.162	0.099	0	-	-	-	-	-	+	-	+
Khaishi	0.042	-0.008	-0.023	-0.010	-0.022	0.093	0	-	-	-	-	-	-	-
Laghami	-0.025	-0.025	-0.042	0.016	0.006	0.027	-0.062	0	-	-	-	-	-	+
Latali	0.016	0.055	0.019	-0.03	0.013	0.204	0.039	0.043	0	-	-	-	-	-
Lenjeri	-0.101	-0.019	-0.071	-0.054	-0.122	-0.034	-0.048	-0.074	-0.064	0	-	-	-	-
Mestia	0.013	0.009	0.005	0.024	-0.037	0.114	0.012	0.002	0.014	-0.079	0	-	-	+
Mulakhi	0.046	0.027	0.010	0.023	0.010	0.123	0.014	0.008	0.033	-0.004	0.002	0	-	+
Tshkumari	-0.011	0.027	-0.003	0.035	-0.006	0.128	0.032	-0.006	0.036	-0.101	0.008	0.057	0	+
Ushguli	0.217	0.084	0.086	0.086	0.133	0.331	0.080	0.172	0.106	0.24	0.119	0.095	0.186	0

Table 6. mtDNA F_{ST} data and MDS plot for the comparison of Svan villages

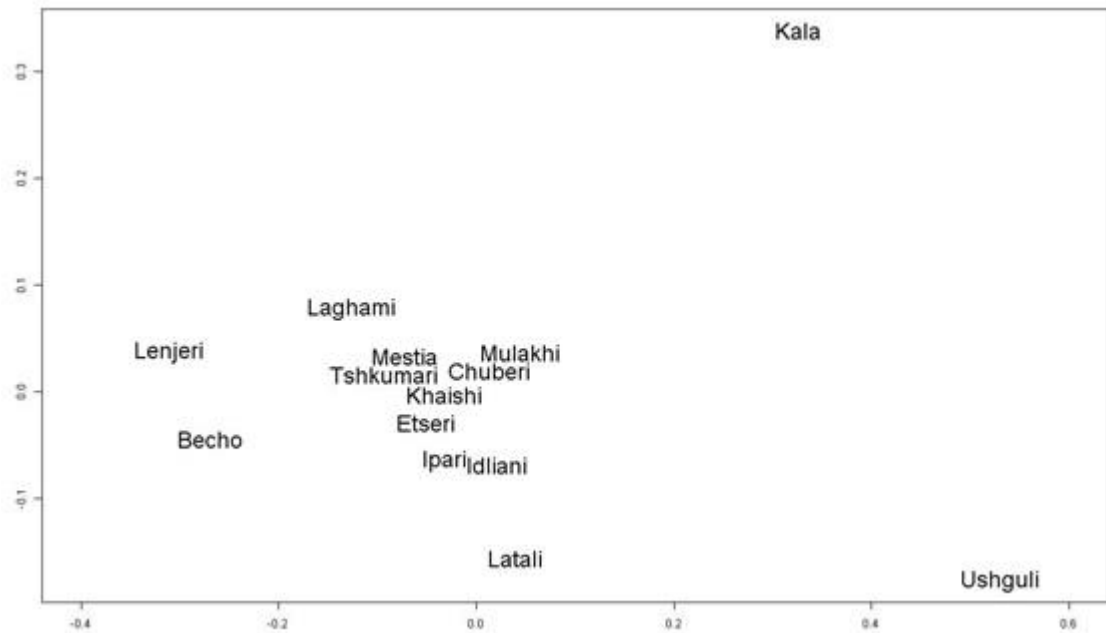


Figure 15. An MDS plot based on F_{ST} estimates generated from mtDNA HVS-I sequences from 14 Svan village districts (based on data found in Appendix 7)

IV.a.4. Phylogenetic Analysis

One noteworthy finding was the high frequency of haplogroup W mtDNAs in the Svans, and in particular W6, which at 11% was the highest percentage ever seen in a single population. For this reason, and because W6 is highly diffuse in Eurasia (Richards et al. 1998), we constructed a network of W6 haplotypes from our own data and published sequence information (e.g., Family Tree DNA; Olivieri et al. 2013; Terreros et al. 2011) to explore its phylogeographic features.

Interestingly, the topology of the resulting haplogroup W6 network (**Figure 16**) did not show any well-defined subclades. Because this network contained so many Svan haplotypes, and because many of the clusters or branches were represented by

single haplotypes (nodes), it was difficult to say much about their regional specificity. Nevertheless, the fact that the haplotypes of neighboring populations were only 1-2 steps apart from Svan haplotypes and that ethnically and geographically diverse samples (i.e., Iranian, Turk, Georgian, Svan) appeared within a single branch indicated the considerable history of movement and dispersal for W6-bearing individuals. Given its diversity, this haplogroup might also have arisen in this region, as W6 is hardly the most widespread of all of the W sublineages observed in human populations (Metspalu et al. 2004). Moreover, none of the branches were entirely without haplotypes from populations residing in the greater Middle East.

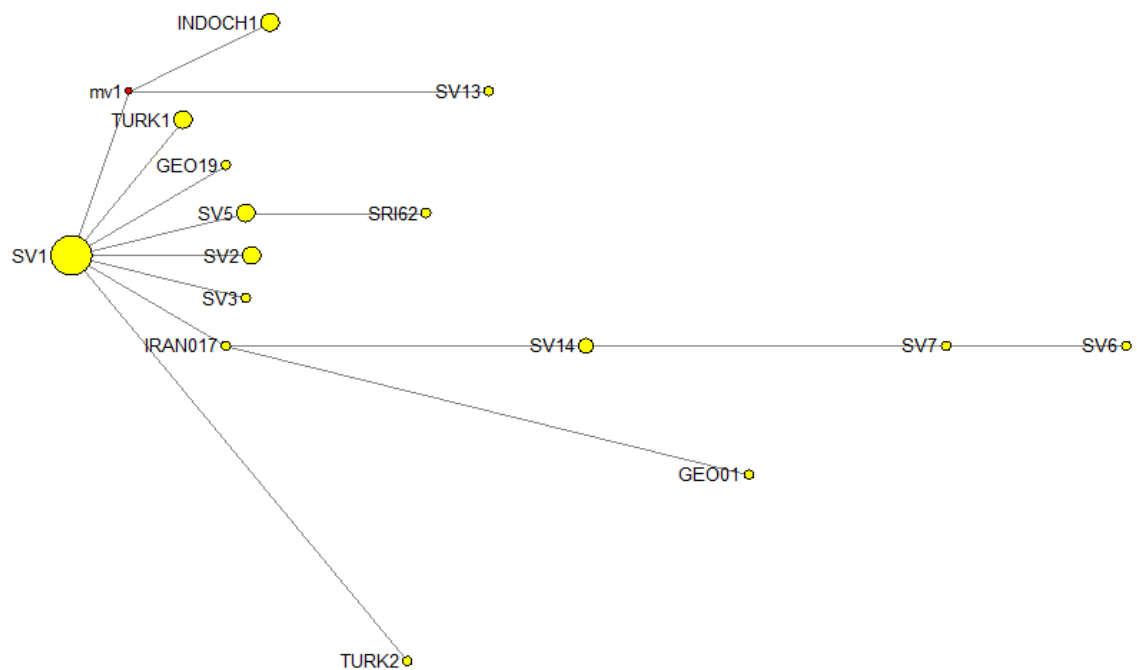


Figure 16. A median-joining network of mtDNA haplogroup W6 HVS-I sequences

Using the evolutionary rate, we calculated a TMRCA for W6 at 20,614 YBP. This date fell within the range of Upper Paleolithic dispersals from the Near East. However, its peculiar geographic trajectory suggested an association with a broad easterly dispersal, perhaps beginning in or near the South Caucasus (see Discussion). Interestingly, our TMRCA date is somewhat older than the estimate calculated by Richards et al. (1998), which was 18,500 YBP.⁷¹

We also constructed a median-joining network for mtDNA haplogroup X2, inasmuch as this multi-branched haplogroup is found within a broad and diffuse Eurasian region (Cui et al. 2010; Reidla et al. 2003). Given the significant presence of X2 haplotypes in Svans, we thought it important to look more deeply into its branching structure (**Figure 17**). In this network, Svan X2 haplotypes did not form a distinct cluster, but were instead dispersed throughout it. The network had two large nodes (EUR1 and EUR2), the latter of which was more clearly the ancestral haplotype. EUR1 included individuals from Iran, Italy and Greece, as well as Armenians, Nogai, Abazins, and Adygei, but no Svans. EUR2 included individuals from France, Iran, Greece, Albania, Turkey, Lebanon, and Georgia, including Svans, and one Nogai. Although difficult to glean anything specific about the geographic origin of such a haplotype, its diversity⁷² is suggestive of an origin in Western Asia well before the Neolithic, and later expansion into Europe and other areas (Reidla et al. 2003). It is also worth noting that no Arabian Peninsular individuals were present within the ancestral node. The

⁷¹ This estimate was based largely on Finnish and other European data available at the time.

⁷² The haplotype for EUR1 = T16189C-C16223T-C16234T-C16278T. EUR2 = T16189C-C16223T-C16278T. Based on a review of the published data, EUR2 appears to be the founder haplotype.

reticulations appearing in this network were likely due to recurrent mutations, such as 16093, 16129, 16192 and 16248, which could not be resolved by adjusting the weighting scheme for HVS-I mutations.

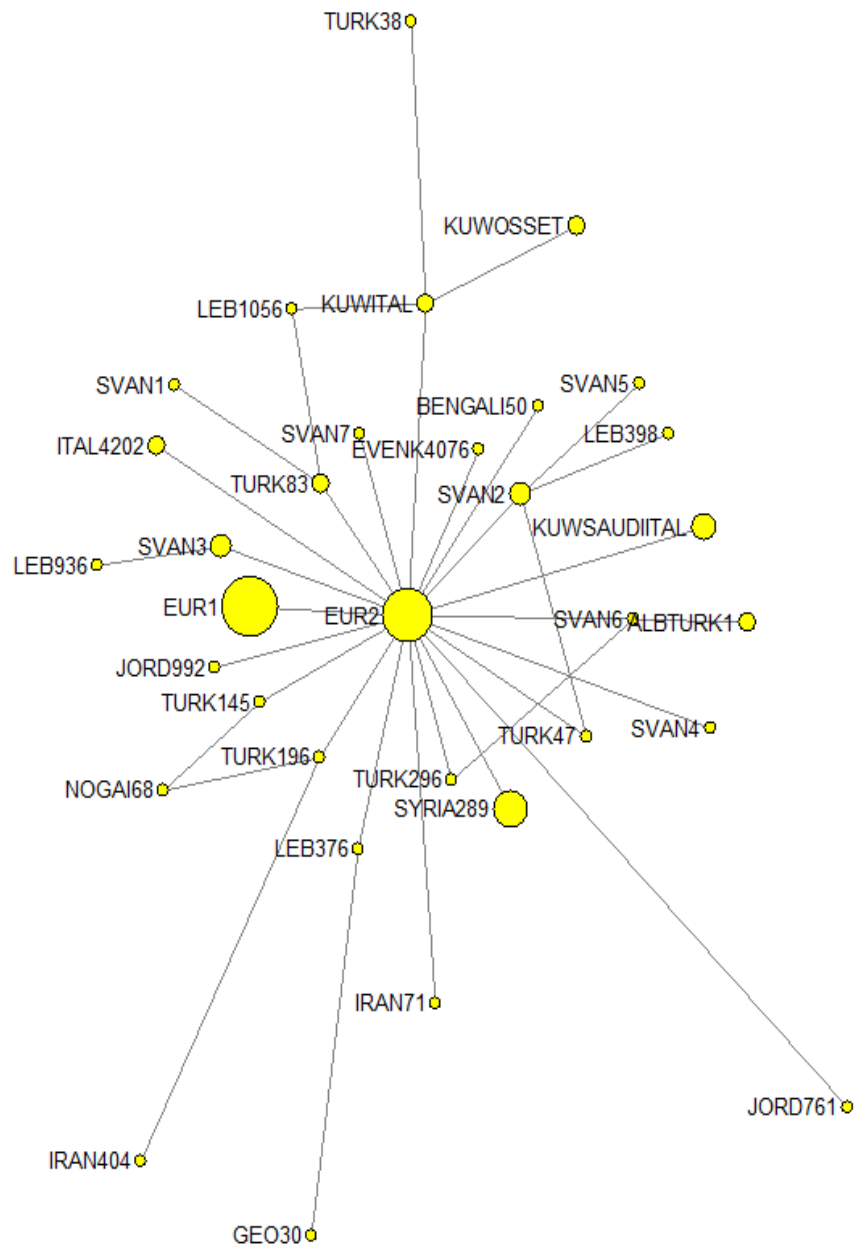


Figure 17. A median-joining network of mtDNA haplogroup X2 HVS-I sequences from Svans and comparative populations

We calculated a TMRCA for X2 at 26,938 YBP. This date also falls within the range of Upper Paleolithic in Europe and the Near East. However, the standard deviation for this estimate was 13,117 years, which is quite large. The upper end of this range would put the emergence of X2 closer to the Middle to Upper Paleolithic transition, while the lower end would place it closer to the Neolithic transition. Given the very broad geographic trajectory of mtDNA haplogroup X, but the relatively limited trajectory of X2 (the Levant, Caucasus, and southern Europe) (Reidla et al. 2003), it seemed reasonable to associate its phylogeographic pattern with Neolithic dispersals.

We generated networks for several less frequent haplogroups (data not shown) present among Svans, and estimated TMRCA for them. These estimates (which were not calculated using other data sets) revealed little more than the coalescence dates for the haplogroups themselves (which are quite similar to other published estimates), not their regional variants/subclades. The TMRCA were as follows: haplogroup H = 41,668 YBP; haplogroup K = 43,940 YBP; haplogroup T = 37,037 YBP; and haplogroup U = 67,309 YBP.

IV.b. Y-chromosome Diversity in Svans

IV.b.1. Haplogroup and Haplotype Diversity

As can be seen from the pie chart of NRY haplogroup frequencies (**Figure 18**), G2a represents 79% of Svan male lineages. The next most common haplogroup was R1a, which comprises 10% of males, followed by J2alb and I2a at 6% and 4% each, respectively, plus a single sample of haplogroup N. Though it is difficult to make any

inferences about population history from a single sample, it is worth noting the likelihood that this single N-bearing individual descends from a lineage originating somewhere in eastern Eurasia (Shi et al. 2013). Since we have mtDNA evidence (i.e., haplogroup C) of Mongol-related settlement in the Caucasus (especially the North) (Новосельский 1948; Kurat 1961; Pritsak 1967), it would appear this historical process has had a minor effect even on this isolated highland population. It is more important, however, to note the lack of East Eurasian-affiliated haplogroups, both mtDNA and NRY, among Svans than their low frequencies of certain types. Whereas in **Appendix 9**, we note the presence of mtDNA haplogroups A-D in several North Caucasus populations, both Caucasian- (e.g., Chechens, Circassians) and Turkic-speaking (e.g., Kabardines, Kara Nogai) groups, the presence of East Eurasian-affiliated NRY haplogroups in the same populations are almost entirely absent (Balanovksy et al. 2011; Yunusbayev et al. 2012).

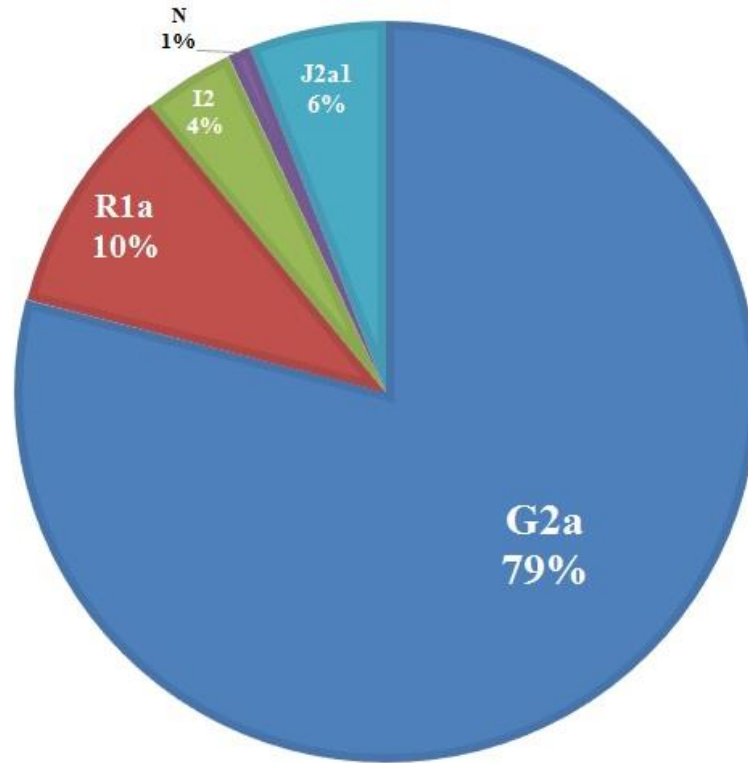


Figure 18. Svan Y-chromosome haplogroup frequencies

The Y-STR data for the 103 Svan males who participated in this project, and their haplogroup classification, are reported in **Appendix 8**. We detected 72 distinct Y-STR haplotypes among 103 male Svan participants. This large number of haplotypes contrasted in interesting ways with the limited set of haplogroups to which they belonged. As we have seen, mtDNA haplogroup diversity among Svans was extraordinarily high, whereas Y-chromosome haplogroup diversity was low. Yet within the majority G2a haplogroup there was, in turn, a great deal of haplotype diversity. While low haplotype diversity may be viewed as denoting the presence of a founder effect, high haplotype diversity generally means some significant amount of time has

passed, allowing it to accumulate, particularly if gene flow from outside groups has been limited. Recurrent gene flow (i.e., the regular introgression and departure of G2a males from the general population) may also be an explanation in this case, although given Svaneti's geographic isolation, this also seems less likely than it might on, say, the open plains of the lowland Caucasus.

The case for a coherent genetic process in Svaneti is further complicated when we compare it to other Caucasus highland (or indeed, 'refuge') areas such as Daghestan. There, haplotype diversity is also high, and haplogroup diversity low, yet socially speaking the region could hardly be more diverse, with scores of languages, hundreds of dialects, and cultural traditions dividing neighbors (Balanovsky et al. 2011; Bulayeva et al. 2002). Svaneti, by comparison, seems monolithic.

IV.b.2. Descriptive Statistics

For this analysis, we carried out statistical analyses using Svan Y-STR haplotype data. Paternal haplotypic diversity in the Caucasus was fairly high overall (**Table 7**), with no population analyzed yielding a diversity index of less than 0.988. The Armenian and Georgian diversity values of 1.0 can, in this sense, be considered anomalous since their sample sizes match the number of haplotypes present in them. The average gene diversity (i.e., the measure of average differences within populations) was not affected by this anomaly. Overall, these figures indicate a lower average diversity within Svans compared to neighboring populations. Perhaps significantly,

Anatolians exhibited a high average gene diversity, a fact which could suggest this as being an important source region for paternal lineages in Caucasus populations.

Population	n	# of haplotypes	Gene diversity	Average gene diversity over loci
Svan	88	72	0.994 ± 0.002	0.511 ± 0.264
Abkhaz	52	46	0.988 ± 0.010	0.661 ± 0.338
Anatolian	171	123	0.993 ± 0.002	0.738 ± 0.365
Armenian	260	260*	1.000 ± 0.000	0.627 ± 0.317
Circassian	132	105	0.996 ± 0.002	0.65 ± 0.329
Georgian	6	6	1.000 ± 0.096	0.682 ± 0.417
N. Ossetian Digor	126	90	0.988 ± 0.004	0.638 ± 0.324
N. Ossetian Iron	229	151	0.988 ± 0.003	0.502 ± 0.258

* Herrera did not respond to an inquiry regarding the sample sizes (*n* value) of his data.

Table 7. Descriptive statistics for Y-STR haplotypes in Svaneti and neighboring regions

It is important to note that high haplotypic diversity in a region with otherwise low haplogroup diversity can point to multiple scenarios. On the one hand, this can indicate the presence of a few old and well-rooted male lineages whose diverse lineages have evolved *in situ*. On the other hand, it may also point to a region geographically prone to accumulating settlers from diverse sources (or source with similar sets of Y-STR haplotypes). The Caucasus would appear in different senses to fit both scenarios, given the history of this region explored in the previous sections, and we further consider these possibilities in the Discussion section.

IV.b.3. Population Subdivision

To investigate population subdivision in Svans based on Y-chromosome data, we estimated F_{ST} and R_{ST} values for NRY haplogroups (**Tables 8 and 9**) and haplotypes (**Appendix 8**), respectively. The numbers in Table 8 are indicative of the relative similarity of haplogroup frequencies. Aside from a single comparative value (Anatolians/Georgians) which was considered insignificant, these numbers indicate moderate to significant genetic similarity between these populations. The highest values (those over 0.4) are suggestive of significant genetic similarity between Svans and Abkhaz, Armenians and Anatolians, and Anatolians with South Ossetians, based on their haplotypes, but regardless of haplotype background. Though these facts are not, in themselves, surprising given the geographic proximity and shared history (more certain in the case of Armenians and Anatolians) of these groups, the similarity of Anatolian and highland Caucasus populations is noteworthy. Higher values (those over 0.3) are suggestive of similarity between Svans and Anatolians and Armenians; Abkhaz with Anatolians and Armenians; Anatolians with Circassians; Anatolians with North Ossetians; and Armenians with South Ossetians. The greatest instance of similarity, not surprisingly, was between North Ossetian Iron & Digor. Here again we note the trend of Anatolians serving as a kind of common denominator for genetic similarity between regional populations. It is also noteworthy that similarity between Georgians and their neighbors is fairly low overall.

The F_{ST} values in **Table 9** depict an entirely dissimilar picture of regional genetic similarity (as based on shared or similar allele frequencies), though one without Anatolians as a proxy. Here, the more noteworthy instances of genetic similarity (over 0.5) involving Svans between with Dargins and Yakuts. In fact, the highest instances of similarity overall (>0.7) occur between these three populations.

	Svan	Abkh	Anat	Arm	Circ	Geo	NOss	SOss
Svan	0.000	+	+	+	+	+	+	+
Abkh	0.439	0.000	+	+	+	+	+	+
Anat	0.357	0.323	0.000	+	+	-	+	+
Arm	0.339	0.338	0.421	0.000	+	+	+	+
Circ	0.193	0.313	0.375	0.121	0.000	+	+	+
Geo	0.201	0.342	0.218	0.161	0.103	0.000	+	+
NOss	0.054	0.364	0.357	0.222	0.146	0.078	0.000	+
SOss	0.095	0.510	0.444	0.386	0.286	0.246	0.071	0.000

Table 8. R_{ST} values estimated from Y-STR haplotype data for Svans and comparative populations. The significance values are shown as pluses (+) and minuses (-), with (+) indicating significant differences at $p = 0.050$. Population Key: Svan=Svans. Abkh=Abkhaz. Anat=Anatolians. Arm=Armenians. Circ=Circassians. Geo=Georgians. NOss=North Ossetians. SOss=South Ossetians.

	Arm.	Bel.	Egy.	Ira.	Leb.	Pal.	Rus.	Sau.	Syr.	Tur.	Uzb.	Yak.	Cir.	Oss.	Che.	Dar.	Avar.	Svan.
Arm.	0.000	+	+	-	+	+	+	+	+	+	+	+	-	+	+	+	+	+
Bel.	0.220	0.000	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+
Egy.	0.161	0.370	0.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ira.	0.001	0.258	0.123	0.000	-	+	+	+	-	-	+	+	+	+	+	+	+	+
Leb.	0.048	0.310	0.093	0.010	0.000	+	+	+	+	+	+	+	+	+	+	+	+	+
Pal.	0.090	0.325	0.127	0.040	0.065	0.000	+	+	+	+	+	+	+	+	+	+	+	+
Rus.	0.187	0.002	0.329	0.217	0.278	0.302	0.000	+	+	+	+	+	+	+	+	+	+	+
Sau.	0.145	0.377	0.225	0.075	0.107	0.016	0.340	0.000	+	+	+	+	+	+	+	+	+	+
Syr.	0.060	0.281	0.172	0.005	0.042	0.020	0.253	0.021	0.000	+	+	+	+	+	+	+	+	+
Tur.	0.014	0.215	0.128	0.007	0.036	0.080	0.199	0.125	0.050	0.000	+	+	+	+	+	+	+	+
Uzb.	0.035	0.115	0.209	0.044	0.099	0.168	0.093	0.213	0.103	0.050	0.000	+	+	+	+	+	+	+
Yak.	0.525	0.555	0.614	0.599	0.522	0.490	0.467	0.574	0.521	0.402	0.465	0.000	+	+	+	+	+	+
Cir.	0.018	0.240	0.255	0.088	0.150	0.171	0.217	0.229	0.147	0.072	0.080	0.494	0.000	+	+	+	+	+

Oss.	0.216	0.484	0.452	0.341	0.370	0.335	0.426	0.426	0.373	0.230	0.342	0.648	0.110	0.000	+	+	+	+
Che.	0.136	0.419	0.337	0.078	0.094	0.196	0.370	0.203	0.126	0.117	0.185	0.596	0.220	0.413	0.000	+	+	+
Dargin	0.300	0.400	0.404	0.267	0.294	0.132	0.351	0.093	0.145	0.256	0.323	0.708	0.342	0.538	0.390	0.000	+	+
Avar	0.211	0.408	0.320	0.173	0.212	0.057	0.366	0.032	0.078	0.176	0.278	0.620	0.264	0.436	0.312	0.067	0.000	+
Svan	0.258	0.456	0.490	0.407	0.411	0.361	0.400	0.464	0.405	0.268	0.348	0.764	0.135	0.050	0.490	0.585	0.479	0.000

Table 9. F_{ST} estimates using NRY haplogroup frequency data for Svans and comparative populations. Significance Level=0.050

An MDS plot based on R_{ST} estimates from Y-STR haplotypes in the Svans and neighboring populations is shown in **Figure 19**. In this plot, the Ossetians clustered close together, and the Svans were positioned about equidistant between Georgians and both Ossetians, with Abkhaz being located farther away. Aside from this seemingly anomaly, the genetic distance between the Svans and other Caucasus ethnic groups corresponded well to the geographical distances between them.

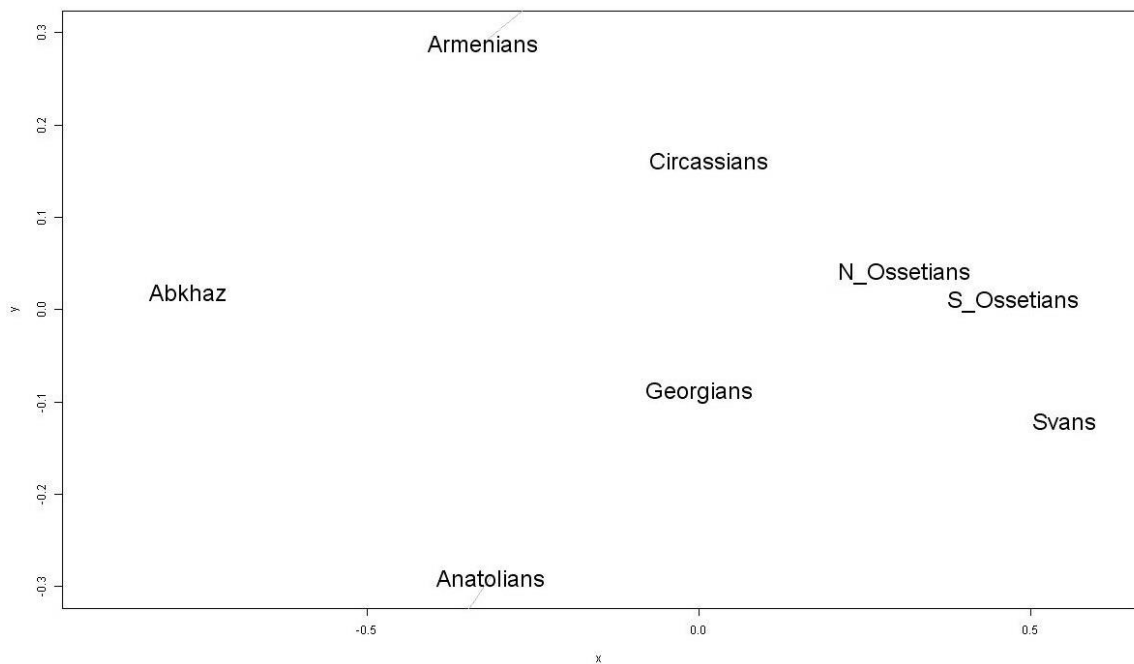


Figure 19. An MDS plot based on R_{ST} values generated from Y-STR haplotype data inclusive of Svans and their Caucasus neighbors

A second MDS plot (**Figure 20**) illustrated the genetic relationships based on F_{ST} estimates between Svans and several regional Eurasian populations. Based on this plot, we observed, primarily, the overall correlation of geography and haplogroup

frequencies, with the interesting exceptions of Chechens and Avars clustering closer to Peninsular Arabians than to their neighbors in Daghestan. This finding is likely explainable by the high incidence of NRY haplogroup J2 in both populations, and indeed in most of the populations in this cluster. The second important observation to be made from this plot concerns the frequencies of Central Asian (i.e., Uzbek) and Near Eastern lineages within Caucasus populations. The presence of R1a among Russians and Belarusians shifted these populations to the upper center, and the presence of N3 among Yakuts likely pulled them into an isolated right-hand position. Those populations with varying proportions of J1, J2, and G2 were situated closer to the center of the plot. Accordingly, the position of Svans as some distant from other populations in the plot was likely indicative of both the high frequencies of haplogroup G and R1a.

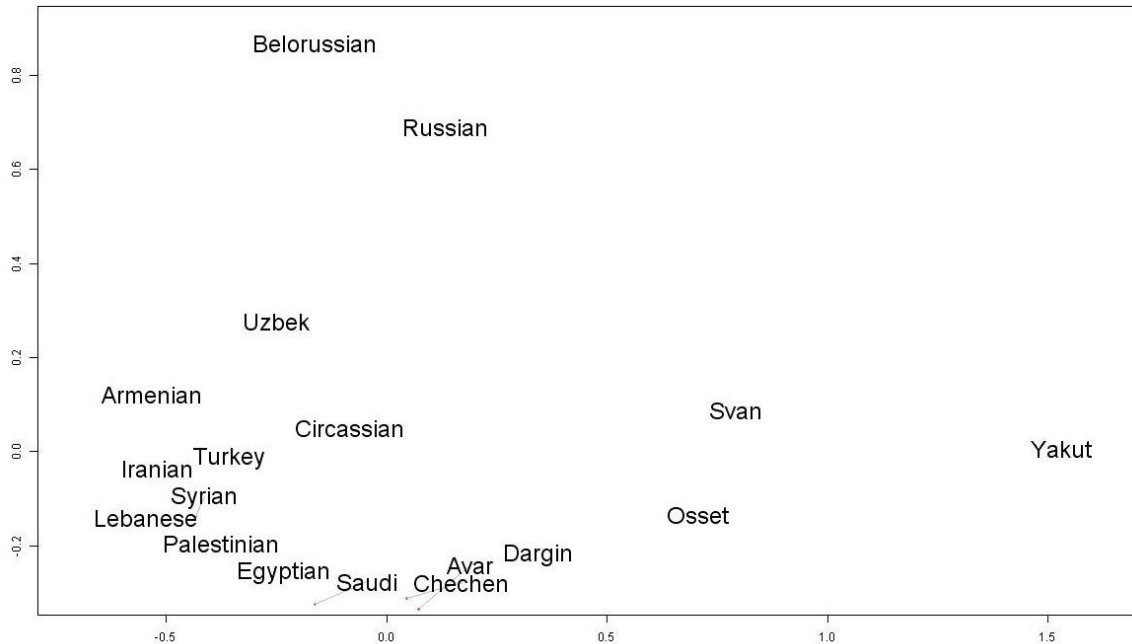


Figure 20. An MDS plot based on F_{ST} values estimated from NRY haplogroups in Svans and other Eurasian populations⁷³

We also analyzed Y-chromosome diversity at the village level in Svaneti using R_{ST} estimates based on Y-STR haplotypes (**Table 10**). Although the sample sizes per village were, in several cases, too small to make statistically significant assessments of them, it was possible to see certain trends in the data. Based on the lack of significance for most of the pairwise comparisons in **Table 10**, as well as the proximity of villages in the MDS plot (**Figure 21**), there did not appear to be any patterning of paternal haplogroup distribution in Svaneti. G2a occurs in Chuberi, a village not far from the border with Abkhazia, as well as in Etseti, another western village in Upper Bal, but also appears in Ushguli, the furthest northeast one can go in Svaneti before losing contact with the Upper Svan communities.

⁷³ Although this plot is generally very coherent, the assumptions of F_{ST} analytics can sometimes create biases that an R_{ST} analysis would not.

	Becho	Chuberi	Etseri	Idliani	Ipari	Latali	Mestia	Mulakhi	Tshk.	Ush.
Becho	0	-	+	-	-	+	-	-	-	-
Chuberi	0.077	0	-	-	-	-	-	+	+	+
Etseri	0.014	0.025	0	-	-	-	-	-	-	-
Idliani	0.053	-0.005	0.003	0	-	-	-	+	-	+
Ipari	0.142	-0.042	0.073	0.26	0	-	-	+	-	+
Latali	-0.056	0.037	-0.019	0.036	0.09	0	-	-	-	-
Mestia	0.047	-0.017	-0.014	-0.011	0.048	0.003	0	-	-	-
Mulakhi	0.116	0.098	0.033	0.274	0.237	0.06	0.033	0	-	-
Tshkumari	-0.004	0.081	-0.027	0.121	0.16	-0.056	-0.006	0.027	0	-
Ushguli	0.059	0.238	0.061	0.304	0.384	0.023	0.148	0.105	0.009	0

Table 10. Pairwise R_{ST} values based on Y-STR haplotype data from Svan villages. The significance values are shown as pluses (+) and minuses (-) in the upper section of the table, with (+) indicating significant differences at $p = 0.050$.

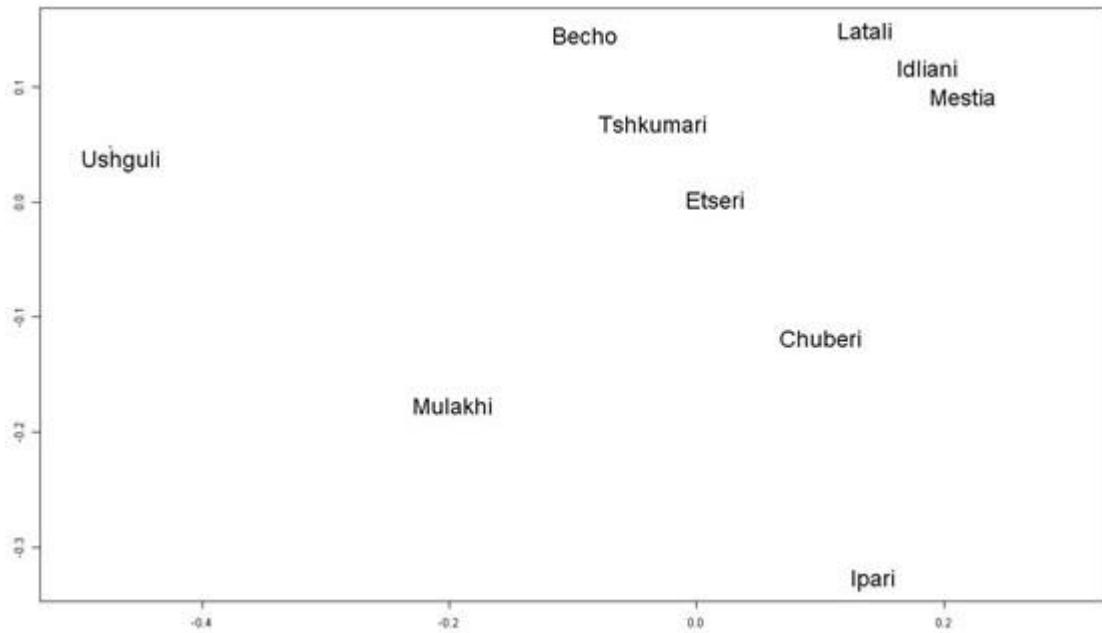


Figure 21. An MDS plot based on R_{ST} values estimated from Y-STR haplotypes in 14 Svan village districts.

Our AMOVA results for Y-chromosome STR haplotype data, which were based on data for Svan and comparative populations, and included Anatolians and Iranians, are shown in **Tables 11** and **12**. The former of these shows results for all populations put into a single grouping, while the latter shows the results for our comparison of North and South Caucasus population structure (Abkhaz, Circassians, Digor North Ossetians, Iron North Ossetians) and South (Anatolians, Armenians, Georgians, Svans) Caucasus populations. Overall, the trend seen in **Tables 11** and **12** suggests population-level differentiation has had a far stronger effect than geography. **Table 11** indicates that more than a third of diversity is attributable to interpopulational differences, while **Table 12** shows that only a small percentage of the variation (1.07%) is due to geographic structuring of populations in North and South. These data were supported by the clustering of Caucasus, Anatolian, Iranian and Levantine populations in the MDS plot shown in **Figure 19**. This finding is perhaps best explained, in turn, by recourse to the distinct histories and structures of the populations within the regional datasets.

Source of Variation	Sum of Squares	Variance Components	Percentage Variation
Among Populations	20866.996	23.32427	36.65
Within Populations	42576.850	40.31899	63.35
Total	63443.847	63.64326	

Table 11. AMOVA results based on R_{ST} estimates using Y-STR haplotypes from Svans and comparative populations

Source of Variation	Sum of Squares	Variance Components	Percentage Variation
Among Groups	4572.367	0.68438	1.07
Among Populations within Groups	16294.630	22.91180	35.85
Within Populations	42576.850	40.31899	63.08
Total	63443.847	63.91516	

Table 12. Results of AMOVA R_{ST} analysis based on Y-STR haplotypes for Svans and comparative populations (inclusive of North-South Caucasus geographic affinities)

IV.b.4. Phylogenetic Analysis

We also subjected the Y-STR haplotype data from haplogroup G2a to phylogenetic analysis using Network 4.6.1. The resulting Svan G2a network (**Figure 22**) is characterized by a complex set of branches. Although lacking a clear central node, the distribution of the 72 haplotypes in the network was extensive. What this network suggested about settlement patterns was not entirely clear. It could reflect evidence of an old lineage with a complex expansion history, and indeed apparently a distinctive one as the number of unique haplotypes shown in **Appendix 9** would suggest. Keeping in mind that the epicenter of NRY haplogroup G2a appears to be the eastern Black Sea area (Rootsi et al. 2012), this observation is further suggestive of a long-standing source population basic to all three highland populations, and from which the slightly lower haplotype diversity among Svans can be attributable to their greater isolation, and gene flow, rather than to a founder effect. In this regard, aside from the

extraordinary number of unique haplotypes in the population, we observe no founder (star radiation) topology evident in the network, such as that seen for so-called ‘Genghis Khan’ star-cluster for NRY haplogroup C*(x3C3c) in Mongols (Zerjal et al. 2003).

As mentioned above, we used both a pedigree-based mutation rate (one mutation per 453 years) and an evolutionary mutation rate (one mutation per 2778 years) to estimate TMCRA for specific haplogroups. For haplogroup G2a, since the nodes of this cluster most central to the network (**Figure 20**) were represented by more than one sample (SV023 and SV028),⁷⁴ we ran the coalescence analysis twice using each one as the founder haplotype. Using the evolutionary mutation rate, the TMCRA for the G2a network using SV023 as an ancestral node was 12,592 years BP, while that using SV028 as the ancestral node was 12,664 BP (**Table 13**).⁷⁵

We also generated a similar Y-STR network for R1a haplotypes (**Figure 23**). While the STR haplotype variation in this network was limited, and indeed much smaller than any other sampled population in the Caucasus having a significant proportion of R1a, this lineage comprised a larger proportion of Svan Y-chromosomes than for most other groups in the Caucasus. Given all the R1a haplotypes are different, it is impossible with so few individuals to make accurate inferences concerning similarities and differences. These inferences are further clouded by a longstanding lack of informative SNP markers that could lead to the geographic source for R1a dispersals (Underhill et al. 2010). Research into the split of European from Asian R1a

⁷⁴ Founder haplotypes are estimated as the median of current haplotypes (Rootsi et al. 2012).

⁷⁵ Given what is known about the time depths for both G2a in the Caucasus and Svan as a language, we believe the pedigree-based mutation rates to be too rapid. Thus, we prefer the evolutionary-based results (**Table 13**).

(Pamjav et al. 2012) and subsequent division into seven smaller regions (one of which is the Caucasus) (Underhill et al. 2015) have revealed the presence of both European and Asian lineages in the Caucasus (see Discussion for more on R1a). Based on the network depicted in **Figure 23**, and using the same mutation rate as employed for G2a above, the TMRCA for R1a was estimated to be 8,334 YBP (**Table 13**).⁷⁶

In addition, we produced a median-joining network for haplogroup I2a Y-STR haplotypes in Svans (**Figure 24**). Its TMRCA was estimated at 11,807 years (**Table 13**).⁷⁷

Haplogroup	Evolutionary Rate TMRCA (YBP)	Pedigree Rate TMRCA (YBP)
G2a	12,592 ± 1781	2,065 ± 313
	12,664 ± 1921	2,051 ± 290
R1a	8,334 ± 2204	1,359 ± 359
I2a	11,807 ± 3331	1,925 ± 543

Table 13. Coalescence time estimates for three Svan NRY haplogroups (see page 118 for an explanation of pedigree vs. evolutionary mutation rates)

⁷⁶ This estimate (8334 ya) is some 16,700 years more recent than Underhill et al (2015)'s estimate of 25,100 ya for the divergence of R1a and R1b. However, the same paper estimates the branching of R1a-M417 to have occurred more recently, i.e., 5800 ya. That our estimate falls between these widely divergent estimates for R1a suggests a broad phylogeographic trajectory for the evolutionary history of this haplogroup.

⁷⁷ There is no specific estimate in the literature for I2a, Underhill et al. (2007) calculated the divergence of subclades I1 and I2 at 28,400 (± 5.1) ya.

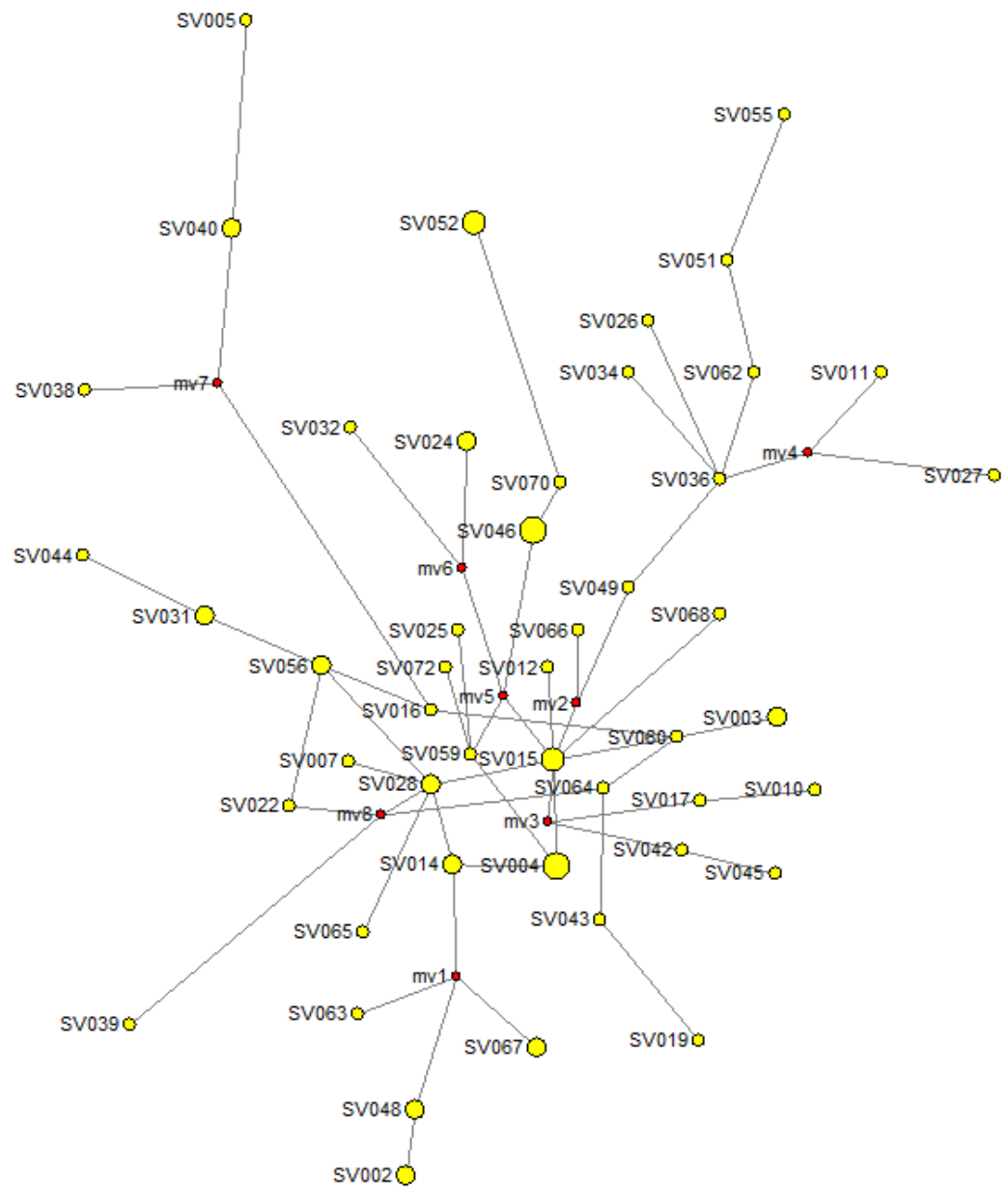


Figure 22. A median-joining network of Svan haplogroup G2a Y-STR haplotypes

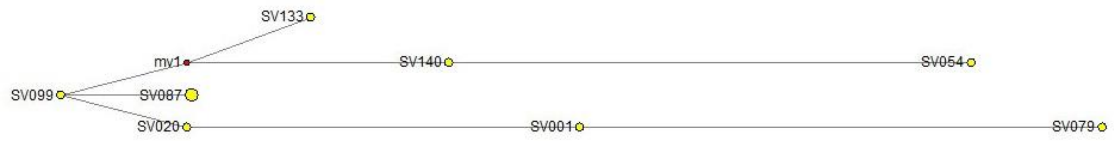


Figure 23. A median-joining network of NRY Haplogroup R1a Y-STR haplotypes

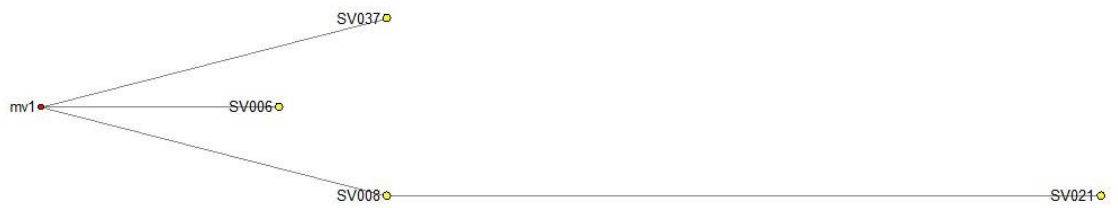


Figure 24. A median-joining network of NRY Haplogroup I2a Y-STR haplotypes

CHAPTER V: DISCUSSION

V.a. Overview

This study provides the first comprehensive survey of mtDNA and Y-chromosome variation in the Svan population of highland Georgia. The South Caucasus, viewed as an extension of the West Asian corridor, may have played a key role in the peopling of the Eurasian steppe, or may have served as little more than a cul-de-sac for post-LGM settlers and nomadic hunters. As such it has, except for periods of glacial inhospitality, experienced punctuated flows of migrants for the last 40,000 years.

In Chapters 1 and 2, we reviewed the events and conditions that are likely to have led to the current mtDNA and Y-chromosome distribution in both the populations of the Caucasus in general, and the Svans in particular. In Chapter 4, we reviewed the results of the statistical and phylogenetic analysis of the mtDNA and NRY data, which characterized genetic diversity in the Svans and their neighbors. Before drawing conclusions as to the implications of these data for the ethnogenesis of the Svan population and the peopling of the Caucasus, we must make some general observations about mtDNA and Y-chromosome phylogeography in Eurasia, as well as discuss the genetic lineages present in the Svans.

The fairly clear pattern underlying mtDNA variation in the Middle East (west of the Indus Valley) includes Anatolia and the Caucasus within it. While western Eurasian mtDNA lineages (N-derived, e.g., H, V, K, T, U, X, J, W) are frequently found past this boundary into South and East Asia, there is an almost total absence of the common South Asian mtDNA lineages M*, U2a, U2b, U2c, U9, R*, R2, R5, R6, N1d, and HV2

lineages in Anatolia, the Caucasus, Iraq, and the Iranian plateau (al-Zahery et al. 2002; Nasidze et al. 2004; Majumdar 2010; Quintana-Murci et al. 2004). The absence of these lineages west of the Indus Valley may be due either to limited back-migration from this region, or to key demographic expansions in the Fertile Crescent and Iran prior to, or in association with, an increase in frequency and diversity of western Eurasian lineages (Quintana-Murci et al. 2004). These observations together would suggest a common Pleistocene or early Holocene origin for modern Anatolian, Iranian, and Caucasus populations.

This is not to suggest the South Caucasus has not experienced gene flow or otherwise undergone differentiation since the establishment of these lineages in the region. Indeed, the low frequency of mtDNA haplogroups J, T1, and U3, which have been proposed as the main lineages associated with Neolithic expansions from the Middle East to Europe (Richards et al. 2000, 2002), are suggestive of some influx of genetic lineages during this period. However, if Neolithic settlement is to be seen in the genetic record of the Caucasus, it will more likely be found in the Y-chromosome lineages, given what is known about male-mediated migration patterns related to farming (Ammerman and Cavalli-Sforza 1984; Balaesque et al. 2010; Chiaroni et al. 2008; Chikhi et al. 1998, 2002; Haak et al. 2010; Lacan et al. 2011). Much of what may be said about mtDNA haplogroup frequencies among Svans may also be seen generally in other regional populations in the greater Middle East. However, a number of important and definitive differences are also in evidence, e.g., higher levels of W6 and X2 among Svans, as well as the presence of seven of nine U haplogroups.

Some general observations about Svan Y-chromosome diversity may be made. As we have already noted, the male-mediated lineages of the Caucasus circumscribe those of its southerly neighbors, Anatolia, Iraq, and Iran, and to a much lesser extent the Russian steppe to the north. This being the case, we might deduce that there has been limited male admixture either within the Caucasus since the arrival of such Y-chromosome lineages as G2a and J2, or between the ethno-linguistic groups after their arrival or emergence there. The somewhat removed position of the Svans in the MDS plot based on Y-STR haplotype data (**Figure 21**) might then be taken to imply long-term isolation from other regional populations, including Georgians. Although the field in **Figure 20** might appear slightly different as an R_{ST} plot, the general proximity of Svans to Abkhaz and Ossetian populations in all of these MDS plots should not be surprising, and is suggestive of a common gene ancestry for these three highland populations (though likely with limited subsequent genetic exchange between them). **Table 12**, which features percentages almost identical to its NRY counterpart (**Table 11**), indicates considerable substructure within populations based on Y-STR haplotype data, but is rather unlike the NRY AMOVA results in that indicates a broad maternal gene pool which likely formed in the Caucasus.

In their combined NRY, mtDNA, and autosomal DNA study, Yunusbayev et al. (2011) drew a similar conclusion about significant cross-Caucasus genetic uniformity and a predominantly Near Eastern origin for the populations. While the Svan data support this view generally, especially the Near Eastern origins aspect, we must learn

more about mtDNA frequencies in both Georgia before we can make specific claims about uniformity.

Below, we review the phylogeographies of the mtDNA and Y-chromosome lineages present in Svans, and from this information glean some perspectives which will help us draw some initial conclusions.

V.b. Mitochondrial DNA data

V.b.1. mtDNA haplogroups H and R0

Most of the mtDNA haplogroups presently found in continental Europe, including H, are thought to have originated somewhere in West Asia (Forster 2004; Richards et al. 1996). Haplogroup H accounts for nearly 40% of the mtDNAs in Europe, declines east of the Bosphorus and the Urals and south of the Mediterranean, but still reaches 10-30% in the Caucasus, Middle East and North Africa (Achilli et al. 2004; al-Zahery et al. 2003; Metspalu et al. 1999, 2004; Pereira et al. 2005; Quintana-Murci et al. 2004; Richards et al. 2000; Tambets et al. 2000). Within haplogroup H, some 100 different subclades have been identified, with hundreds of further sub-branches being also being present, based on mitogenome sequences (van Oven and Kayser 2009).

Although the highest frequency of the most ancestral form of H (H1) occurs among Slavic- and French-speakers, haplogroup HV, the parent lineage for H, occurs at its highest percentages in Anatolia and the Caucasus (Malyarchuk et al. 2008), reaching 7% among Armenians (Ottoni et al. 2011), 7% among Georgians (Tambets et al. 2000),

and nearly 10% among Iranian Azeris (Asgharzadeh et al. 2011). This is somewhat higher than in continental Europe, where HV reaches no more than 7% anywhere except for Finland, where, curiously, it reaches 12% (González et al. 2003), presumably due to a founder effect. In Iraq, percentages of HV are even higher, at nearly 13% (Ottoni et al. 2011; but see al-Zahery et al. 2003 for contrasting findings). Intriguingly, although HV occurs up to 7% in Georgians and Armenians, it does not occur at all in the Svans.

mtDNA haplogroup R0 (formerly known as pre-HV; Torroni et al. 2006) is the precursor of HV, and thus has a genealogical connection to the larger ancestral macrohaplogroup R. R0 reaches its highest frequency (38%) on the island of Soqatra, which is formally part of Yemen (Černý et al. 2009), and also shows its greatest haplotypic diversity on the Arabian Peninsula (Achili et al. 2007). This pattern suggests that R0 may have originated and spread from there. The dates for the origin of this haplogroup vary (23.6 – 54.9 KYA; Soares et al. 2009; 10 – 18 KYA; Brandstätter et al. 2008), but occur before the Neolithic period. Therefore, if it is, indeed, the case that R0 spread northward from the Arabian Peninsula into the Levant, Iran and Anatolia, and perhaps bore witness the rise of permanent settlement, food production and animal husbandry in those regions, then the rise of HV must have occurred in one of these places, as well. The not insignificant frequency of HV in several Caucasus populations, and even R0 (pre-HV) among Armenians (<1%; Tambets et al. 2000) and Azerbaijanis (4%; Ottoni 2011; Richards 2000), but the almost complete lack of V, is instructive as

to the likelihood that H and V diverged in, or closer to, continental Europe itself.⁷⁸

Given the paucity of R0 in Anatolia and Iran, it is difficult to identify the population interactions which may have resulted in the presence of this haplogroup in the Caucasus. However, the same may be said about several of the haplogroups found at moderate to high frequencies there.

Regardless of this issue, haplogroup H is thought to have originated somewhere in the Near East 25 – 30 KYA (Achilli et al. 2004; see also Roostalu et al. 2007). It is the most common mtDNA haplogroup in the Caucasus (reaching 15-30% among both North and South Caucasus populations), followed by haplogroups J, K, T, and U. Haplogroups H* and HV*, which together represent nearly half of the Armenian mtDNAs, are maternal lineages otherwise almost exclusively associated with Paleolithic Europe. Recent research on the autochthony of Armenian populations in Anatolia (Ottoni et al. 2011) suggests the divergence of H took place somewhere in this region. This lineage is thought to have spread into Europe gradually, possibly in conjunction with the expansion of the Gravettian Culture (Pereira et al. 2005; Richards et al. 2000), and ultimately expanded to represent more than a third of the European mtDNA gene pool.

⁷⁸ This fact is also a matter worth further consideration vis-à-vis theories of a Holocene expansion of HV from a Franco-Cantabrian glacial refugium (see Achilli et al. 2004; Loogväli et al. 2004; Pereira et al. 2005; Tambets et al. 2004; Torroni et al. 2001). If, following the retreat of Eurasian continental ice sheets some 20-15 KYA, groups of people who had been previously forced south into the Iberian Peninsula and Italy began to expand into central and northern Europe, a significant amount of back-expansion into the Near East must have occurred to permit current percentages of H without V. A more central geographic point for the divergence of HV from R0 (i.e., somewhere in the eastern Mediterranean, probably Anatolia), makes more sense for its distribution than Iberia (see Loogväli et al. 2004; Pereira et al. 2005; Richards et al. 2000; Torroni et al. 1998).

At present, H1 and its sub-haplogroups are found predominantly in Western Europe (see Gonzalez et al. 2003; Mishmar et al. 2003; Pereira et al. 2005; Quintana-Murci et al. 2004; Richards et al. 1998; Simoni et al. 2000; Torroni et al. 1998), although also appearing at considerable frequencies among North African populations (Brotherton et al. 2013; Ottoni et al. 2010; Roostalu et al. 2007). The presence of this lineage in the Caucasus does not exceed 10% in any single population in the North or 5% in any population in the South (Ottoni et al. 2010).

On the other hand, certain sublineages of H, including H2, H4 (Pereira et al. 2005), H5 (Roostalu et al. 2007), H6, H7, H8, H13 (Pereira et al. 2005), H20 and H21 (Roostalu et al. 2007), are all found primarily in the Caucasus. Curiously, some of them also occur among Basques, which would suggest vestiges of very early circum-Mediterranean travel (see Sánchez-Velasco and Leyva-Cobián 2001 for an opinion to the contrary). Other sublineages of H (e.g., H1, H11, H18) are found in Europe, the Levant, North and West Africa, and the Arabian Peninsula (Ottoni et al. 2010; Pereira et al. 2005; Ennafaa et al. 2009). Each of these H subhaplogroups has a different expansion time and trajectory. For example, the age of H13 has been estimated at 24.3 KYA, H4 at 27.5 KYA, H6 at 26.6 KYA, and H21 at 17.7 KYA, based on HVS-I sequence data (Roostalu et al. 2006).⁷⁹ Since coalescence estimates cannot by themselves help us determine dates of population expansions into specific geographic locales, we cannot be sure whether these pre-LGM, pre-Holocene dates are indicative of a very early expansion into the Caucasus or later diffusion into the region. The

⁷⁹ The age estimate for H13, when counting only synonymous substitutions is 18,500 KYA (SD 6,600) and 10,100 KYA (SD 6,000) for H4 (Roostalu et al. 2007: 442), both occurring prior to the Holocene.

occurrence of H in Svans is limited to the ancestral H (and one additional H27 sample, as well as the CRS), without discernable sub-branching.

V.b.2. mtDNA Haplogroup U

The presence of mtDNA haplogroup U mtDNAs in the Svan population is intriguing for several reasons. Chief among these is the fact that almost all of the known sub-branches of U are present among them, excepting U8 and U9. The former of these two is found among Basques, Italians in Jordanians (González et al. 2006), while the latter is limited to East African and South Asian populations (Quintana-Murci et al. 2004). The numerous subgroups of U are widely distributed across Eurasia, including among some found only among Indian tribal populations (Kivisild et al. 1999a, 2000). Several of its branches (U1, U2, U4) are shared between West and South Asia (Metspalu et al. 2004; Quintana-Murci et al. 2004), while others are more strongly associated with Europe (U1, U4, U5)⁸⁰ and North Africa (U6; Maca-Meyer et al. 2003). U3 is found generally in Europe, the Near East, North Africa, and the Caucasus, with some subclades specific to each of these regions, and others spread across all of them (Quintana-Murci et al. 2004; Richards et al. 2000). U7 has a similarly broad phylogeographic Eurasian trajectory, but one that seems to peak (and perhaps originate) in Western Asia (Metspalu et al. 2004) and also include Siberian tribes (Derbeneva et

⁸⁰ Recently, excavated remains from the St. Augustine convent in Goa were subjected to DNA analysis. The results yielded a unique form of U1b, which is otherwise absent in India, but attested in the Caucasus. Corroborating literary evidence surrounding the relics, the authors (Rai et al. 2014), propose them to belong to Queen Ketevan of Georgia.

al. 2002a, 2002b, 2002c; Kivisild et al., 1999; Richards et al. 2000) and Sri Lankan Veddas (Ranaweera et al. 2014).

The available TMRCAs are instructive concerning the age and dispersal of these lineages. Basal haplogroup U* dates to 51,000 – 67,000 YBP (Achilli et al. 2005; Kivisild et al. 1999b), and thus its emergence is contemporaneous with the initial spread of AMHs across Eurasia. Its presence in aDNA from Upper Paleolithic and Epipaleolithic European samples (Bramanti et al. 2009; Behar et al. 2012; Richards et al. 2000) also supports a very early divergence event. Richards (1998) has dated U5* to 50,000 YBP, and more importantly, Metspalu et al. (1999) calculated the expansion of U3* in Armenians, Turks and Georgians at $29,500 \pm 5,000$ YBP, which occurs well before the LGM. Quintana-Murci, et al. (2004) calculated the time-depth for U7* (without 16309) at $35,100 \pm 8,500$ YBP, and for U7a (with 16309) at $22,500 \pm 5,400$ YBP.

Geographically speaking, U is a haplogroup with a continuous presence across Eurasia, from Iberia to Baikal—an expanse which also happens to be the ‘Caucasoid’ trajectory in the Classical sense (Bamanti et al. 2009). That all these U haplotypes, with their differing ages, would converge in Svaneti is worth noting. Since the numerous branches of U have various branching dates—some separated by 10,000 years—and thus do not have a single geographic point of dispersal, it is all the more beguiling to find some many collected in a single population. Indeed, the Svans may demonstrate the most U haplotype diversity of any single population of comparable size. According to van Oven et al. (2009), the defining mutations for haplogroup U are 11467, 12308

and 12372. These distinguish it from its parent, macrohaplogroup R. Were the Svans descended from the population in which U split from R, we might expect to find these mutations present among them. However, none of these are present in among Svans, even in those haplotypes classified as U*.

It is interesting to note that, while many of these very old maternal lineages are shared between ethnolinguistic groups in the Caucasus (thus supporting our argument for maternal descent from Epi- or Upper Paleolithic populations of the region), two specific populations share mtDNA haplogroups in such a way that something more is revealed about their histories. Except for the presence of haplogroup N, the Ossetes have much in common with Armenians in term of their maternal gene pool. Is it a coincidence that Armenian and Ossetian are the sole Indo-European languages spoken in the Caucasus, and are both considered relatively ‘late’ arrivals in the region compared to other languages? Do these populations instead represent a more autochthonous range of maternal lineages in spite of their linguistic affiliations?

Although we acknowledge that both Armenians and Ossetians have historical cultural-linguistic ties to greater Iran⁸¹, the former to the south, the latter to the north, this explanation for shared haplotype and haplogroup frequencies may, in fact, be specious. While classified as a dialect of Persian until the late nineteenth century (Hubschmann 1962), Armenian is fundamentally distinct from other Indo-Persian languages, although it has absorbed a great deal of Persian vocabulary during its time as an imperial subject (especially during the Arsacid Dynasty), and neighbor to Persia

⁸¹ According to some researchers, they share much in common with each other (e.g., Абаев 1970, 1978).

(Saryan 1982: 14). However, consideration of the deep histories of these two populations and their respective ethnogeneses only draws them further apart. As discussed above, Armenians are a population phylogeographically rooted in central or eastern Anatolia (Herrera et al. 2011), regardless of the origin of the Armenian language. By contrast, the Ossetic language is the sole living member of the Scythian subgroup of the Eastern Iranian subfamily, which also includes Yagnobi, Wakhi, Parachi, and Pushto (see Morgenstierne 1973; Schmitt 1989).

The presence of Ossetian-speakers in the Caucasus is a phenomenon not fully understood. Based on current evidence, it is not certain that their presence is due to population processes originating north of the Caucasus rather from the south, as the traditional version of their history would suggest. The word “Osset” is an adopted exonym via Russian from the Georgian ოსო (sing.), ოსებო (pl.), a term used since the Middle Ages to refer to the Iranic-speaking peoples of the northern mountains. Moving further back in time, this term may have its origins in the Alan endonym “As”. The endonym that became an exonym later became the endonym again, as the Ossetians lacked a defining term for themselves even in the years prior to incorporation into the Russian Empire (Shnirelman 2006: 40).

The extent to which the Ossetes are descended from the Alans is uncertain, but there are few other explanations for the presence of an Eastern Iranian language in this region of the Caucasus. The Alans were, allegedly, either a cohort or a component of the tribes known exonymically in Greek Classical literature (e.g., Herodotus, Pliny the Elder, Eudoxus of Cnidus), as well as Chinese dynastic chronicles (see Alemany 2000:

396-434) as Sarmatians, who settled in the North Caucasus during Antiquity (Sulimirski 1970; see also Klaproth 1822). The Hellenic historian Amianus Marcellinus describes the Alans as living along the river Tanais (now, the Don) in the fourth century AD. But, by the 10th century CE, they had occupied the greater part of the region and established a state, one that later, in the 13th century, suffered at the hands of Mongol invaders. The Alans were pushed south into the mountains, where they allegedly blended into the local population (whose linguistic identity is unknown, but possibly were Dvals⁸²) and later were reborn, at least in linguistic terms, as the Ossetes (Korobov 2011; see also Hirth 1885: 139 note 1).⁸³

V.b.3. Haplogroups J and T

Comparatively little research has been carried out on the branches of these two mtDNA haplogroups within the purview of their presence in the Caucasus. Similarly, no one has undertaken a comprehensive founder analysis for the European iterations of these haplogroups (although Richards et al. 2000 does assess J and T lineages as contributing to the Neolithic settlement of Europe). However, their long-term presence

⁸² Dvaleti and Dvals are attested in Old Georgian annals; see Thomson 1996: 65, 880, 261), a Medieval Armenian geography (see Hewsen 1992: 116), and at least one Classical source (see Tardy 1978). Although these accounts are not always in agreement, or necessarily precise, according to them, Dvaleti would have been roughly synonymous South Ossetia as it is today. The word ‘Dval’ survives in numerous place names and surnames among Georgians and Ossetians (Кузнецов 1992). Their linguistic categorization of the Dval language is disputed, with some researchers associating it with Kartvelian (Топчিশвили 2009), and others with Nakh languages (Меликишвили 1962; Гамрекели 1961). An Indo-European (i.e., Iranian, and therefore pre-Ossetic) theory has also been proposed (Кузнецов 1992).

⁸³ This version is also consistent with that of the Georgian epic, *The History of Vaxtang Gorgasali* (see Thomson 1996). The ethnogenesis of Ossetians is surely a complex topic, one made even more so by nationalist and separatist rhetoric. In linguistic terms, at least, the connection between Alans and Ossetians is hardly controversial. Hirth (1885) furthermore identifies the Alans with the Aorsi (Ἄορσοι) mentioned in Tacitus (*Annals* 12.15), Ptolemy (*Tetrabiblos* 3.5) and Strabo (*Geography* XI:V: 8).

in the Middle East is well known, as the Jordanian population sampled by Gonzalez et al. (2008) had haplogroups J and T at about 6% and 10%, respectively.

Coalescence time estimates for these lineages all suggest their presence in the Near East well before the LGM. Metspalu et al. (1999) calculated the expansion of T among Armenians and Georgians at 27 KYA, while also citing an estimate by Richards et al. (1998) for T1 at 9 KYA. They calculated the same time depth (27 KYA) for haplogroup J*, which has otherwise been estimated at 8 KYA in Europe (Richards et al. 1998). Similarly, the coalescence date for mtDNA haplogroup W has been estimated at 25 KYA by Torroni et al. (1996). While it is difficult to explain these wildly divergent dates without re-running the analyses with the original HVS-I data, it may at least be observed that many of these lineages must have originated among Upper Paleolithic hunter-gatherers in Anatolia, Iran, and elsewhere in the Near East.

V.b.4. Haplogroup W

A frequently occurring macrohaplogroup R-derived haplogroup in India and the Caucasus is W. While haplogroup W occurs at 5% in northwestern India (i.e., Gujarat, Kashmir, and Punjab), elsewhere in India it appears at extremely low frequencies (from 0% to 0.9%) (Metspalu et al. 2004; Quintana-Murci et al. 2004). The presence of haplogroup W in the Caucasus is made doubly intriguing by its near absence in the European subcontinent, except among central-northern Finns (9%; see Finnilä et al.

2001).⁸⁴ Its frequency is also high in Iran (13%) and Pakistan (10%) but declines in Central Asia (5%).

Given the estimated time depth for W6 of 20,614 YBP, and the diversity that has accumulated, it is intriguing that this haplogroup is not more widely dispersed, especially in Europe. If W6 originated in Anatolia or Iran during the Upper Paleolithic, then it should have spread both east and west along with most other mtDNA haplogroups of equivalent time depth. While acknowledging that NRY and mtDNA lineages have very different kinds of histories, and that the latter do not gloss onto Paleolithic and Neolithic human population movements in the same way as the former, it is still reasonable to ask why W6 did not spread further west. One reason may be that its movement was initially restricted by glacial ice, and subsequently by isolation in the Caucasus highlands.

An additional observation about the distribution of W6 is its correlation with the Indo-Persian sub-branch of the Indo-European family of languages. Being present in two Iranians, one Gujarat, and one Sinhala-speaker from Sri Lanka, it is not unreasonable to suppose that W6 travelled along with the spread of the proto-languages of this family. The presence of several W6 individuals in Turkey and one in Xinjiang do not necessarily fall outside the Indo-Persian sphere either, given what we know about both the geographic trajectory of the Persian sphere (Balanovsky et al. 2015; Morgenstierne 1973) and the expansion of Turkic languages within this sphere (Golden

⁸⁴ Yet, it is absent among Volga Finno-Ugric speaking populations (Bermisheva et al. 2002).

1992; Yardumian and Schurr 2011). Unfortunately, a TRMCA for the emergence of these few specific haplotypes would produce too wide an error margin to be useful.

With the hypothesis of a Caucasus highland-based origin for W6 in mind, we must then wonder why W6 is not more common even among long-standing North and South Caucasus populations. W, its parent lineage, is present at low frequencies among most Caucasus populations (Nasidze et al. 2004a), but W6 is nearly absent outside Georgia. Furthermore, the frequency of W6 in Svans is the highest of any population worldwide. Further sampling in Georgia may help to elucidate this question. The fact that the ancestral haplotype (SV1) consists of four Svans, one Slovak, one Turk, one Iranian, one Galician, and one Piedmont Italian suggests a distribution inclusive of several key areas associated with Neolithic and post-Neolithic expansions. Interestingly, the ancestral haplotype contains no Eastern Eurasian individuals, which is further suggestive of two separate demographic events at work. There is one anomaly contained within the W6 network. In the 16192 branch containing Iran01, SV14, SV7, and SV6, the C16292T mutation appears twice. This observation suggests that the second of these is a recurrent mutation (though atypically so).

V.b.5. Haplogroup X2

As suggested above, the phylogeographic diversity of individuals contained in the ancestral haplotype EUR2 (as well as in the EUR1 branch), and the distribution of haplotypes radiating from the latter of these two is suggestive of Western Asian Neolithic dispersal pattern. This supposition is supported by the analysis of mtDNA

haplogroup X by Reidla et al. (2003), who posit that the phylogeographic distributions of X and U are consistent with the initial dispersal patterns of AMH. Although Reidla et al. (2003) do not directly relate the distribution of X2 to the expansion of Neolithic farmers, they do claim that the diversity of X2b is consistent with a more general postglacial population expansion in western Eurasia (as well as North Africa). The presence of X2 in Iron Age and other premodern European burial contexts (Deguilloux et al. 2010; Gómez-Sánchez et al. 2014; Lacan et al. 2011) is also well established. Its complete absence from Northern Europe (Reidla et al. 2003) would suggest that its distribution began no earlier than the transition to farming. This distribution has also led some researchers (e.g., Fernandes et al. 2012) to propose a European origin for X2. However, this is unlikely given the presence of X2 in fairly high concentrations in the Caucasus, as well as the distinctive form of X2a is known in the Americas (Brown et al. 1996; Fagundes et al. 2008; Reidla et al. 2003). Such a pattern is left to European-origin-proponents to explain how individuals bearing X2 haplotypes travelled more than 5000 miles over glacial ice.

Given the coalescence estimate for haplogroup X2 as 21,600 YBP (Reidla et al. 2003), the beginning of X2a's journey to the Americas could not have occurred prior to the LGM. Thus, its phylogeographic range in Eurasia, including a significant presence in the South Caucasus, is most likely a product of post-glacial expansions from the Near East, especially those associated with the expansion of agricultural populations. Given the phylogeographic contents of the ancestral haplotype EUR2 of our X2 network (especially the lack of Peninsular Arabs), we propose an origin for this haplogroup

among Anatolian or northern Levantine hunter-gatherers who, following their transition to agriculture, took it with them west and east.

V.b.6. Summary

More research into the sub-branches of these low frequency mtDNA haplogroups is required before assessments can be made as to the directionality of their flow into the South Caucasus, or the timing of their entries and expansion histories. Although they may not appear now to play an important role in the peopling of the Caucasus in general, and the ethnogenesis of Svans in particular, they should not be forgotten when constructing a model for the initial peopling of Western Asia. The fact that R-derived haplogroups are found everywhere in Eurasia suggests the divergence of R (following that of M and N; Álvarez-Iglesias et al. 2009; Palanichamy et al. 2004) must have occurred prior to the spread of AMH across the globe (Richards et al. 2006: 237). This inference can be reconciled with dates for R* in South Asia, and thus may be considered to have been part of early Eurasian expansion events. This leaves the question as to whether the Caucasus mtDNA U and W lineages can also be traced to pre-Holocene settlement, or instead were later (i.e., Neolithic) arrivals from the Middle East or Anatolia.

V.c. Y-chromosome Data

The preponderance of NRY haplogroup G2a in Svans and other populations of the highland South Caucasus is a fact that will dominate any discussion of the origins of

and interactions between these populations. While this lineage is quite significant, the minority haplogroups are also of importance in unraveling the story of Svan history and ethnogenesis. The presence of J2a1 (and conspicuous absence of J1) and R1a (and absence of R1b) are particularly significant. All four of these haplogroups have played an important role in the settlement processes of the Near East and greater Eurasia. Their relative frequencies in Svans and proximate populations in the Caucasus are discussed below.

V.c.1. Haplogroup G

Haplogroup G-M201 is a curious lineage inasmuch as it is found across the Old World, including Western Europe, Siberia, Afghanistan, Sri Lanka, and Malaysia (Di Cristofaro et al. 2013; Hammer et al. 2006; Rootsi et al. 2012), and yet the date of its emergence from NRY haplogroup F* has been estimated to be as recent as 9,500 YBP (Cinnioğlu et al. 2004). While it is possible for such a wide distribution to have occurred since the Neolithic, the overall low global distribution everywhere (except the Caucasus) of G-M201 makes an older date such as 17,000 YBP (Semino et al. 2000) more reasonable.

A satisfactory date for the emergence of haplogroup G is important in this context because it affects the dating of its downstream lineages, and interpretation of their histories. If, as Cinnioğlu et al. (2004) suggest, G* emerged only 9,500 YBP, then this lineage was likely brought into the region during the Neolithic or through later settlement processes involving haplogroup G-bearing males in the Caucasus. Another

possibility to consider is the emergence of G in the Caucasus region itself. However, given the specificity of certain G haplotypes among Caucasus populations and the rarity of ancestral forms in the literature on the Caucasus (e.g., Balanovsky et al. 2011; Yunusbayev et al. 2012), this scenario is less likely than its emergence somewhere nearby (Iran, Anatolia), followed by its migration into the Caucasus. Although there are insufficient dates for the emergence of either G* or G2, we do have estimates for sublineages G2a1-L293 and G2a3b1-P303 [now called G2a2b2a] (also the most frequent and widespread G sub-haplogroup overall), which together account for nearly all G haplotypes in the Caucasus. The TMRCA for G2a3b1-P303 is 12,095 YBP and that for G2a1-L293 is 9,400 YBP (Rootsi et al. 2012). Among Abkhazians, G2a3b1-P303 occurs at 24% in Abkhazians, 39.7% in Adyghe, and 36.5% in Circassians. In addition, it occurs at 17.8% among Palestinian Arabs, whereas, in continental Europe, this lineage does not exceed 6% (Rootsi et al. 2012).

Various sublineages of G2 occur throughout Turkey (Cinnioğlu et al. 2004; Gökçümen et al. 2008), especially along the southern Black Sea Coast (Balanovsky et al. 2011: 2912). In the Balkans, the frequencies of haplogroup G and its derivatives are also high, but unevenly so. For example, in Osijek, a town in northeastern Croatia, G2a* occurs in 13.8% of males living there (Battaglia et al. 2009), whereas it only appears at trace frequencies among other Croats, Bosniacs, Bosnian Serbs, and Slovenians.⁸⁵ According to a spatial autocorrelation analysis of G2 subclades (Rootsi et

⁸⁵ The reasons for this peculiar Croatian G2a frequency are probably lost to unrecorded history. Nevertheless, it makes a compelling case for combined high-resolution NRY analysis combined with detailed historical and ethnographic research. Battaglia et al. (2009) do not speculate on these reasons.

al. 2012), no clinal patterns exist in the overall G2 distribution. This observation suggests that the G2 distribution has been shaped by isolation by distance and demographic complexities rather than recent unidirectional migration and settlement.

Although the age of G2a-P15 remains unclear, its sublineage G2a1a-P16 has been dated to 9,600 YBP (Rootsi et al. 2012). The presence of G2a in Neolithic Europe is well attested through aDNA studies (Haak et al. 2010; Lacan et al. 2011; Vanek et al. 2009). In fact, the majority of recovered Y-chromosomes from European Neolithic burials been shown to belong to G2a-P15, thus allowing the case to be made for its association with Neolithic settlement patterns.⁸⁶ If its point of origin is indeed further east, perhaps in Iran or the South Caucasus, then the question then becomes whether G2a3b1-P303 and G2a1a-P16 may be said to be contemporaneous, or indeed spring from a common source in the Caucasus or elsewhere in the circum-Black Sea region. G2a occurs at significant frequencies in Abkhaz and Circassian populations, both Northwest Caucasian-speaking groups, and thus perhaps represents a northwest Caucasus/Black Sea littoral-centered lineage (Rootsi et al. 2012; Balanovsky et al. 2011).

⁸⁶ Derenburg Meerestieg II, a Linearbandkeramik (LBK) Neolithic cemetery in northern Germany. Though the G2a-P15 individual could not be dated by radiocarbon method, other skeletons there dated to between 5,100 and 6,100 YBP (Haak et al. 2010). In addition, aDNA at Avellaner Cave in northeastern Spain has tested positive for G2a-P15. The burial context from which it was recovered has been radiocarbon dated to about 7000 YBP (Lacan et al. 2011). Furthermore, Ötzi the Iceman belongs to NRY haplogroup G2a2b (Keller et al. 2012). Semino et al. (2000) associate G and J2 with agricultural spread, but alternate explanations, implicit and explicit, exist (e.g., Yunusbaev et al. 2012; King et al. 2008; Cinnioglu et al. 2004; Semino et al. 2004; Zalloua et al. 2008; King et al. 2011.) Rootsi et al. (2012) consider G2a3b1c-L497 to be autochthonous to Europe and thus associate it with the LBK culture of Central Europe.

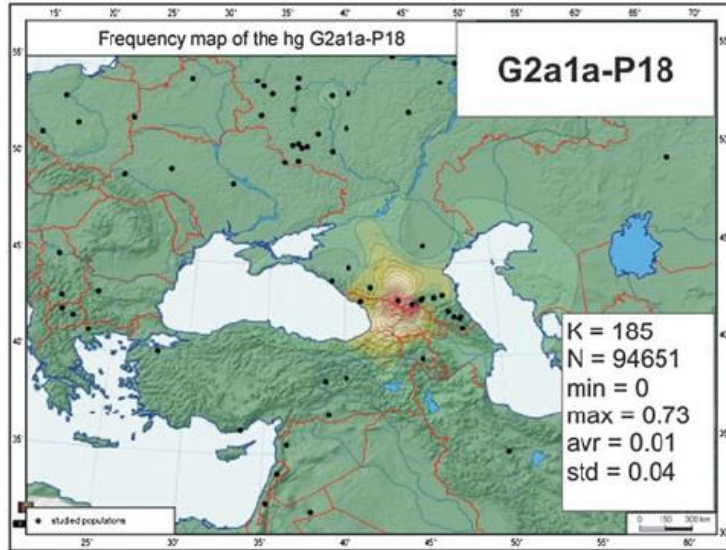


Figure 25. A frequency map of NRY haplogroup G2a1a (Balanovsky et al. 2011)

NRY haplogroup G2a3b1-P303 reaches its highest frequency along the eastern shores of the Black Sea and in the northwest Caucasus, appearing as far east as Ossetia, where G2a1a-P16 becomes prevalent (Balanovsky et al. 2011; Rootsi et al. 2012) (**Figure 25**). This research has thus far yielded a high incidence of G2a among Svans. However, no samples have ever been taken in Racha (the region between Svaneti and Ossetia) to determine to what extent these two G2a haplotypes overlap regionally, or are demarcated by social or topographical boundaries. Outside of the Caucasus, G2a1a-P16 occurs at significant frequencies (21%) in only Anatolia, parts of Russia, and Spain, while being virtually non-existent elsewhere. Its estimated coalescence date of 12,095 YBP is important because it falls within the range of the early Holocene in the Near East, and thus may have emerged in the right place at the right time to fundamentally shape the peopling of the Caucasus, maybe also eastern Anatolia.

The preponderance of G2a3b1-P303 in the northwest Caucasus is also marked by lower haplogroup diversity there (Rootsi et al. 2012) compared with Anatolia and Armenia, suggesting that G2a is likely did not emerge in Abkhazia or Ossetia, in spite of its high frequencies at least in the latter (**Figures 24 and 25**). Given this higher subgroup diversity coupled with deep basal branches of G known in Iran, Armenia, and eastern Anatolia (Rootsi et al. 2012), G2a seems more likely to have originated there and expanded into the central Caucasus highlands during the Epipaleolithic or later. On the other hand, G2a1-P16 is effectively Caucasus specific and amounts to nearly one-third of the Caucasian males, in both the south and northwest Caucasus. Whether this is due to a founder effect or some other process is as yet known. Given that haplogroup G frequencies drop to zero between the northwest Caucasus and the Eastern European steppe to the north, it is highly unlikely that G2a-bearing males arrived from the north (Balanovsky et al. 2008; Kharkov et al. 2004). Perhaps significantly, Maikop sits in the center of haplogroup G2a3b1-P303 frequency distribution. Although the area was likely heavily populated by the time this Bronze Age archaeological horizon took form, the frequency of this haplotype in the Caucasus may possibly be related to the Maikop phenomenon. Follow-up work to this dissertation will further delineate the Svan NRY haplotypes through SNP genotyping using markers not covered in this study. This work will help determine the sublineages present within haplogroups such as G2a and R1a.

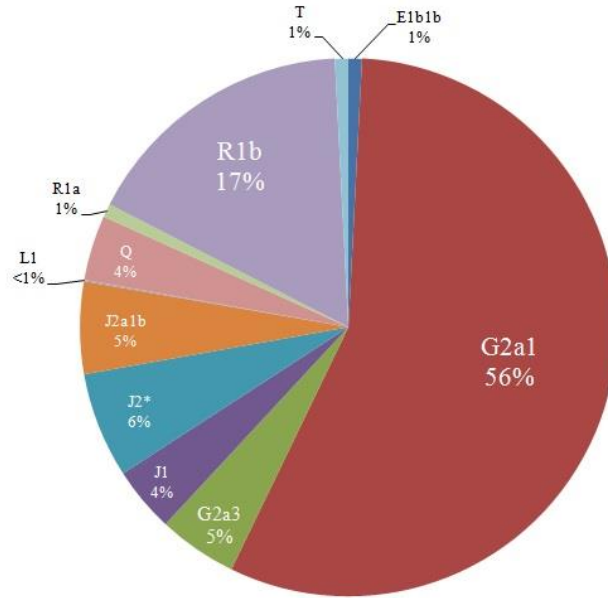


Figure 26. North Ossetian (Digor) NRY haplogroup frequencies (generated from data reported in Balanovsky et al. 2011)

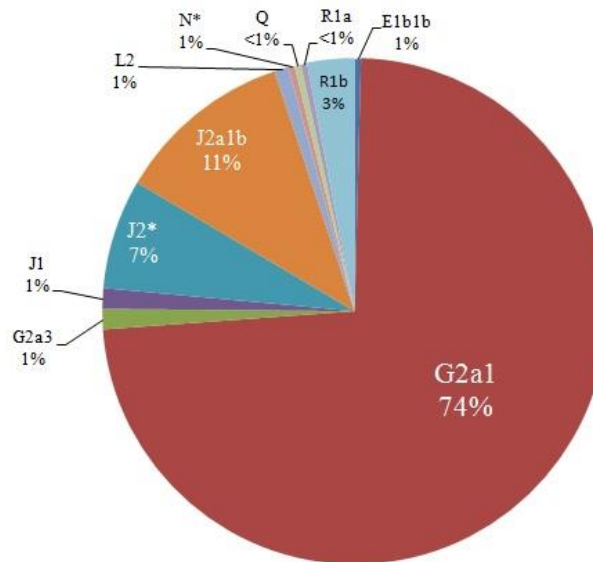


Figure 27. North Ossetian (Iron) NRY haplogroup frequencies (generated from data reported in Balanovsky et al. 2011)

The closely related haplotype G2a3a-M406 (Rootsi et al. 2012) occurs at its high frequency in the Mediterranean and Central Anatolia, especially Cappadocia (~6%), and is not found in regions with significant G2a3b1-P303 frequencies. The expansion time of G2a3a-M406 in Anatolia has been estimated at 12,800 YBP (Rootsi et al. 2012). This date, like that of G2a2b1-P303, falls within the range of the early Holocene in the Near East and the climatic changes which permitted sedentary hunter-forager settlements and proto-Neolithic settlements at key sites such as Göbekli Tepe. G2a3a-M406 also has a moderate presence in the Greek Peninsula and the Peloponnese, as well as in Italy (with a time depth of 8,100 YBP, which may correspond with maritime Neolithic settlement from Anatolia or the Levant (King et al. 2008). Rootsi et al. (2012) estimate that G2a3a-M406 expanded from Iran around 8,800 YBP, a time correlating with the first Neolithic settlements in the Zagros. Thus, this lineage is a candidate for studies of Neolithic expansions, either from Iran to the Mediterranean, or from Anatolia to the Mediterranean and Iran.⁸⁷

Interestingly, the majority of the Ossete Y-chromosomes belong to G2a (Nasidze et al. 2004b, 2008). This haplogroup is found virtually nowhere in the vast territory once considered Alania, Sarmatia, or Scythia, or in the areas of Eastern Europe to which the Alans voluntarily or were forcibly migrated by the Huns (see Alemany 2000: 30-78). These findings indicate that G2a1a is a native central Caucasus

⁸⁷ The distribution of G2a2b2a1a1-M527 in southern Italy, Ukraine, and among the Druze and Palestinian Arabs of the Levant suggests it also has a connection with Neolithic and/or post-Neolithic expansions in the Mediterranean world. Rootsi et al. (2012) estimate the expansion time of this haplotype to be 7100 ± 2300 YBP, and thus believe it to be consistent with a Late Neolithic expansion, perhaps one even associated with the Sea Peoples. Its presence in Ukraine may reflect Metal Age colonization from Anatolia or the Aegean, or some lesser known phenomenon.

haplogroup, and the presence of the Ossetian language there is due to a linguistic shift, perhaps due to an elite dominance process.

If the male-mediated lineages of the north-central Caucasus highlands remained, as it appears, largely unchanged by historical population dynamics, perhaps the maternally inherited lineages also remain largely unchanged since very early times. Perhaps the best explanation for the striking mtDNA affinities between these two populations, Ossetes and Armenians, is geographic. In other words, they could represent vestiges of a pan-Caucasus mtDNA gene pool established well before the advent of any of the current ethno-linguistic groups.

The question as to how the Caucasus fits into these various scenarios of the timing and directionality of Neolithic expansion is as yet unresolved. An answer to this question depends on answers to numerous subquestions, such as when and where G2a1 split into its daughter lineages (a, b, c, etc.), whether more ancestral forms of G2a are to be found in Anatolia or Iran, and whether the Kartvelian language family has any genetic signatures associated with its expansion that can be traced to either Iran or Anatolia. Until populations from Georgia and eastern Anatolia are more completely sampled and analyzed, we must wait for answers to those questions.

V.c.2 Haplogroups R1a and R1b

The presence of haplogroup R1a in the Caucasus is not insignificant. In fact, it appears at frequencies ranging from 33.8% among Karachays (Yunusbayev et al. 2012) to less than 1% among Svans, and among their Ossete neighbors (Balanovsky et al.

2011). For a haplogroup so closely associated with the Eurasian spread of Indo-European language and culture (Underhill et al. 2010), its near absence among Ossetes and Armenians (compared to R1b at 29%), the two Indo-European-speaking peoples in the Caucasus, is worth mentioning. However, this point may actually be less significant than it would seem, since we may be dealing with a form of language and culture shift over time in both cases.

In the case of R1a, the various hypotheses as to its ultimate origin have placed it everywhere from the Baikal region to Ukraine to the South Caucasus (see e.g., Haak et al. 2015; Sharma et al. 2009; Underhill et al. 2010; 2012; Zerjal et al. 2002; Dulik et al. 2012). R1a is a large and diverse NRY haplogroup containing 38 subbranches. Among these is R1a1, a recent branch with a geographic trajectory essentially limited to western and central Europe (Rozhanskii and Klyosov 2012). Of the R1a1 samples analyzed by Pamjav et al. (2012), 98% belonged to one of three sub-haplogroups, defined by the M458, Z280 and Z93 SNPs, respectively. R1a1-M458 appears at its highest frequency in Hungarians (both in Hungary and in Romania), while it is virtually absent in Asia (see also Underhill et al. 2010). By contrast, all Malaysian Indians belonged to R1a1-Z93. Central Asia seems to be where R1a1-Z280 and R1a1-Z93 overlap, in spite of the low frequencies at which they were observed there (Pamjav et al. 2012). These results confirm an earlier and similar study by Underhill et al (2010), which concluded that R1a1a* originated in the broad expanse of Inner Asia, most likely Central Asia and the Altai, spreading possibly with Kurgan cultures into the Caucasus and Eastern Europe. The exclusive presence of R1a1-M458 in Hungary (see Völgyi et al. 2009) further

suggests a Central Asian or southern Russian steppe origin for this lineage, as opposed to a source area in Ukraine. Only further analysis of R1a subclades, especially those appearing in Paleo-Siberian and Finno-Ugric populations, will reveal whether its presence in the Caucasus is due to the incursion of individuals associated with the Kurgan culture, or a more complex process involving both processes.

The vast Old World trajectory of haplogroup R1b and its geographically heterogeneous frequencies makes it difficult to define a point of origin for this lineage. Its sublineage R1b1a2 (R-M269) occurs at 92.3% in Wales and 81.3% in Catalonia (Balaesque et al. 2010), and at 34.4% among Bashkirs from Abzelilovsky District (Лобов 2009), while R1b1c (R-V88) occurs at frequencies as high as 95.5% among Ouldémé-speakers in northern Cameroon (Cruciani et al. 2010). Myres et al. (2010) interpret the phylogenetic relationships of R-M207, its parent lineage, as being indicative of a West Asian origin for R1b, with a relatively rapid subsequent spread of R-M269 into Europe. The timing of the emergence of the R-M412 (R-L51) lineage is also unclear, as this lineage separates the majority of Central and West European R1b lineages from those of Eastern Europe, including the southern Russian plains, and the trans-Urals Siberian lowlands, the Near East, including the Caucasus, and Pakistan. Myres et al. (2010) suggest the R-M412 frequency distribution in Europe is similar to the trajectory of Linearbandkeramik (LBK) wares, and thus a result of a key wave of Neolithic expansion.

The incidence of R1b in Caucasus populations is often inversely proportional to the incidence of R1a, although both are found in moderate frequencies among some

populations, while others possess almost none at all (compare data from Balanovsky et al. 2011 with Yunusbayev et al. 2012). Thus, a certain bifurcation of Caucasus populations emerges. Those with significant frequencies of R1a but minimal R1b include Kabardins, Karachays, Circassians, Abazins, and Adygei—all residents of the northwest Caucasus—whereas those with significant R1b and minimal R1a include North Ossetians (Digor) (**Figure 25**), Armenians, Avars, Bagvalals, Lezgins (in both Daghestan and Azerbaijan), and Tabarasans. Those with equal but low R1a and R1b frequencies include Georgians, Abkhaz, Balkars, Kumyks and Laks. Those with insignificant frequencies of both haplogroups include Rutuls, Dargins, Ingush, Chamalals, Chechens, Andis, Kaitaks, Shapsugs, and North Ossetians (Iron) (**Figure 26**), and Kubachi—all residents of the northeast Caucasus. Unfortunately, the Azerbaijani data of Nasidze et al. (2004) was only resolved to R* and thus cannot be compared to these other data sets.

Given the phylogeographic pattern of these R1 subclades in the Caucasus, it is possible to infer low to moderate admixture from early R1a-bearing steppe populations of those of the northwest Caucasus, especially given the infrequency of R1a in Anatolia, the Levant and Iran (Underhill et al. 2015). The patchy distribution of R1b from eastern Anatolia and Armenia to North Ossetia and Daghestan is more difficult to attribute to any single known historical process, but could be used as a model for vestiges of pre- or early agricultural (even Epipaleolithic) settlement process beginning in Anatolia. The higher occurrence of R1b (24.3%) in highland Syunik (southern Armenia) and Karabakh (14.0%) and its dearth in the Ararat Valley (Weale et al. 2001; Herrera et al.

2011), suggests that the distribution of R1b in the Caucasus is not so much horizontal (east-west) as it is vertical (north-south). Highland regions often serve as refugia for biological and cultural traits, which are more subject to exogenous demands in the unprotected lowlands. Since the most reliable current estimate for the age of R1b puts it at 8,870 YBP (Myers et al. 2011), it is perhaps the oldest of the common NRY haplogroups occurring in the Caucasus, and thus may have been part of a gradual removal to the highlands as other settlement processes unfolded.

V.c.3. Haplogroups I, J1 and J2

The question of the origins of NRY haplogroup J must be first considered in the context of its putatively Upper Paleolithic split from haplogroup I. Two coalescence estimates have been offered for ancestral haplogroup IJ, these being 38,500 YBP (Karafet et al. 2008) and 24,000 YBP (Rootsi et al. 2004).⁸⁸ In spite of the rarity of haplogroup IJ*, this lineage is supposed to have evolved somewhere in western Asia, possibly Iran (Grugni et al. 2012). Haplogroups I and J have subsequently come to dominate almost mutually exclusive domains of Eurasia. Haplogroup I reaches its highest frequencies in the Balkans and Scandinavia, and occurs at moderate frequency in Anatolia, but is largely absent east of the Caspian, and in Africa (Rootsi et al. 2004). By contrast, haplogroup J occurs at its highest frequency in southern Arabia, Sudan, the Sinai, and Daghestan, with only a moderate presence in southern Europe (Balanovsky et

⁸⁸ Prior to the discovery of IJ-M429*-bearing individuals, the existence of this haplogroup nod could only be inferred from the fact that certain mutations are shared in common among all Y-chromosomes belonging to haplogroups I and J (see Grugni et al. 2012).

al. 2011; El-Sibai et al. 2009; Karafet et al. 2008; Sengupta et al. 2006). These distributions suggest that I and J split some time prior to the LGM, with their subclades spearheading two separate settlement processes (Grugni et al. 2012).

The coalescence time for haplogroup I has been estimated at 22,200 YBP, a date that coincides roughly with the LGM (Rootsi et al. 2004), and possibly with the expansion of Gravettian culture (Semino et al. 2000). The age for haplogroup J* has been estimated at 40-10,000 YBP (Di Giacomo et al. 2004: 366) and 31,700 YBP (Semino et al. 2004: 1026). The coalescence times for the daughter lineages of haplogroup J, J1 and J2, have been estimated at 24,100 and 18,500 YBP, respectively, and are thought to have originated in greater Mesopotamia (Cinnioğlu et al. 2004; Semino et al. 2004). If this is the case, then these haplogroups could well be associated with the Neolithic arrival of human populations in the Caucasus.

If we presume that these paternal lineages arose around 15,000 YBP, it is not clear how we can reconcile such age estimates with the conclusions (see below) made by Bulayeva et al. (2003, 2004) based on mtDNA data, especially given the high levels of haplogroup J1 in Daghestan populations⁸⁹ (**Figure 9**). This interpretation is

⁸⁹ Two parallel mtDNA studies of Daghestan populations (Bulayeva et al. 2003a, 2003b), though at lower resolution than that of Balanovsky et al. (2011), confirm the autochthony of several regional populations. According to it, the mean pairwise mtDNA sequence divergence in Daghestan is “higher than that of all other European populations, suggesting that the Daghestan populations were established earlier than those of Europe” (Bulayeva et al. 2003b: 847). This is, according to the authors, “in accord with the observation that Daghestan populations are not part of the large scale cline across Europe thought to represent the expansion of Neolithic farmers” (Bulayeva et al. 2003b: 845). The HVS-I mtDNA data for this study was drawn from five Daghestan population centers: Kubachi, Novo-Kurush, Novo-Mehelta, Urkarah, and Stalskoe. The Alu insertion frequency data was drawn from a partially overlapping sample of populations from five Daghestan populations: Kubachi, Novo-Kurush, Novo-Mehelta, Urkarah, and Stalskoe, as well as Alu insertion frequencies in a partly overlapping sample of populations: Kubachi, Urkarah, Stalskoe, Nogais, and Makhachkala (Bulayeva et al. 2004: 838-39). Of these, only Makhachkala is an urban center of significant size. The rest are regional centers and villages.

supported by a previous study with similar broad conclusions regarding five major ethnic groups in Daghestan (Avar, Lak, Dargin, Tindal, and Kumyk), namely the geographically restricted nature of certain populations (e.g., Bulayeva et al. 2002). As far as genetic affinities between the five groups are concerned, Laks, Dargins, and Avars share affinities with one another, while the Kumyks (a Turkic-speaking people) are relatively distant from other highland populations of Daghestan, an observation explainable by the ancestors of the Kumyks arriving later in the area and likely being Mongol-derived. However, Kumyks share a statistically significant percentage of haplotypes with Dargins, perhaps because a Dargin-related substrate is present in the deep history of Kumyk ethnogenesis, or because of the proximity of Kumyk and Dargin auls (Bulayeva et al. 2003a: 75). The Tindals were also genetically remote from other Daghestan ethnic groups, but showed affinities to Dargin and Avar populations (Bulayeva et al. 2003a). The reason for the genetic affinities between Tindals and Dargins is thus far unclear, given their respective population histories.

If Bulayeva et al.'s (2003, 2004) conclusions are correct, and it is indeed the case that certain mtDNA lineages were established in the northeastern Caucasus prior to the settlement of continental Europe, then we must wonder whether the dominant NRY haplogroup J1*-M267 also arrived there at this time (i.e., the Upper Paleolithic) or later. There are several ways to approach this problem, one of which is to try and correlate genetic and glottochronological data. According to Balanovsky et al. (2011), the northwest and northeast Caucasian genetic-linguistic lineage split occurred prior to 3,000 YBP, followed by a Nakh-Dagestan split around 3,000 YBP. Given the

correlation of these lineage splits with the geography of the Caucasus, it is difficult to imagine them occurring in another setting and shifting neatly into their current places. If this correlation is correct, then the dispersal of a J1*-M267-bearing population settled in or near their current homes at least 5,000 YBP. The pairwise mtDNA sequence divergence results from Bulayeva et al. (2003a, 2003b) further suggest that Daghestan populations were established earlier than those of Europe. If this was, in fact, the case, then evidence of this settlement survives only, at present, in the mtDNAs of the current occupants of this region. Whether this is an indicator of female autochthony and male-mediated immigration is an as yet unresolved, but important, question.

CHAPTER VI: CONCLUSIONS AND FUTURE DIRECTIONS

VI.a. Conclusions

We began this dissertation by posing three interrelated objectives about biological ancestry, history and geography in the Caucasus. The overall directive was to document, for the first time, biological diversity in Svaneti. Although particularly high levels of genetic diversity were evident in Svan maternal haplogroup lineages, this is also generally true of populations from the Caucasus, Iran, and eastern Anatolia. Although haplogroup diversity among males was very low, haplotypic diversity was moderately high. While we cannot from these data alone conclude that Svan populations originated from Neolithic and pre-Neolithic settlement events, we can make inferences about their ancestral history from both the assignment of TMRCAs to the major mtDNA and NRY lineages found in the Svan community, as well as the various statistical analyses that we performed.

High levels of genetic diversity are sometimes indicators of long-term community duration *in situ*, and limited gene flow due to isolation. On the other hand, isolation tends to foster genetic drift which, combined with endogamy, can reduce variation over time. While assigning an time estimate for the emergence of the ancestral Svan community does not necessarily help us track their ethnogenesis against known technological horizons, and climatological, linguistic, or historical patterns, it can do other work. For example, given the phylogeography of NRY haplogroup G2a, we may be in the position to address major regional population settlement events during

the Upper Paleolithic, Neolithic, and Metal Age, as well as the putative 'Alan migration' in the 4th century AD.

Our TMRCA (12,592/12,664 YBP) estimates for NRY haplogroup G2a are suggestive of an origin for the majority of Svan lineages in the Epipaleolithic. The overall pattern of G2a in the Caucasus, and among Svans, may be interpreted as a genetic signal of the expansion of early Neolithic settlers from the Black Sea coast and nearby lowlands following the retreat of the glaciers in the Caucasus. Although the ancestors of all G2a-bearing Svans may have dwelled in lowland Georgia, eastern Anatolia, or beyond, their close relationship to their descendants' current highland neighbors in the Caucasus is suggestive of a nearby geographical locus. Given the low Y-chromosome haplogroup diversity and high haplotype diversity, it is reasonable to posit a long-term evolutionary period for haplogroup G2a among Svans, perhaps beginning in the late Epipaleolithic or early Neolithic of the South Caucasus. However, the overall diversification process of G2a in the Caucasus promises to be revealed as something more complex, such as male movements in and out of the region.

The TMRCA estimates for R1a (8,334 YBP) and I2 (11,807 YBP) haplotypes are likewise suggestive of a late Epipaleolithic and/or early Neolithic origin for them, and thus an association of these lineages with settlement and food production. However, unlike G2a, it is much less certain that these NRY haplogroups emerged in the Caucasus per se. Since the highland Caucasus regions currently inhabited by Svans and Ossetes, and to some extent Abkhaz, are not conducive to sustained agriculture, although perhaps favorable to certain forms of animal husbandry, these populations may

have developed in lowland Samegrelo, Guria, and along the Black Sea coast of Abkhazia during the formative years of the late Epipaleolithic and early Neolithic of western Georgia. However, since there are no reliable glottochronological estimates for the Kartvelian language family, the ethno-linguistic character of these early settlers cannot be delineated with certainty.

The association of Svan and most all South Caucasus maternal lineages with the greater Near Eastern mtDNA lineage distribution further confirms the view that the former groups originated predominantly in the latter region. Although this claim has certainly been made before (Balanovsky et al. 2011; Yunusbayev et al. 2012), our statistical analyses of the mtDNA data confirms that a great deal of genetic variation is shared not only between the North and South Caucasus, but with Anatolian, Iranian, and other Near Eastern populations. Under the present analysis, we cannot be certain of the extent to which multiple expansions from the Near East contributed much or little to the haplotype diversification process. It does seem, however, that we can consider the Svans and their highland neighbors to be part of the overall Near Eastern gene pool.

Our second objective was to compare the gene diversity of Svaneti with that of its western and eastern neighbors, Abkhazia and South Ossetia, respectively. Our Y-chromosome MDS plots, as well as median-joining networks, indicate a close common ancestry for Svan, Ossetian, and Abkhaz male lineages, in spite of their speaking languages from three distinct families. Although it would be premature to suggest this putative common ancestral population emerged in the highlands, we can be sure these lineage distributions were established well before the appearance of the current ethno-

linguistic groups in the Caucasus, and that these cultural groupings have had minimal effects on subsequent gene flow in the highlands. On the other hand, strong Y-chromosome affinities between eastern and western neighboring populations (i.e., Ossete and Abkhaz, respectively) point to a common source population, in spite of their linguistic differences at the language family level.

An unintended though fascinating consequence of this work has been to confirm that the putative ‘Alan migration’ was more of a cultural transition than an actual large-scale migration. The majority of Ossetian Y-chromosomes belong to G2a (Nasidze et al. 2004b, 2008). Since this haplogroup is found virtually nowhere in the vast territory once considered Alania, Sarmatia, or Scythia, or in the areas of Eastern Europe to which the Alans voluntarily migrated or were forcibly moved to the Huns (see Alemany 2000: 30-78), it would seem the male-mediated lineages of the north-central Caucasus highlands remained largely unaffected. These findings support the view that G2a1a is an autochthonous central Caucasus haplogroup, and the presence of the Ossetian language there is due to a linguistic shift.

By contrast, maternal genetic diversity was remarkably high in Svans, indicating a more diverse source population(s) for this ethnic population. It also pointed to the possibility of greater exchange of mtDNA lineages between highland Caucasus regions due to bride theft, patrilocality and other cultural processes that have traditionally restricted male, but encouraged female, gene flow. The reluctance among Svans to marry someone sharing a surname going back ten generations (Tuite 1994) may have led to the necessity of finding women/wives outside the region, but this still cannot

account for the incredible mtDNA diversity in this small population. Future studies might focus on mtDNA diversity in lowland Georgia (Samegrelo, Guria and Adjara), in Abkhazia, and eastern Anatolia to clarify the source of these mtDNA haplotypes. As we have seen, there is a great deal of similar diversity in matrilineal genetic diversity in the Caucasus, but also some very important aspects of distinctiveness, such as the unusual proportions of haplogroups W6 and X2, as well as the presence of seven of the nine U haplogroups.

Our third objective was to examine whether Svan genetic variation is structured by regional residence within Svaneti, which could potentially explain patterns of regional settlement. As can be seen from the MDS plots, there was no geographic patterning of mtDNA and Y-chromosome diversity within Svaneti at the village level. Therefore, we may conclude that any regional mtDNA or Y-chromosome patterning that may once have existed (such as that which has been observed for NRY lineages in Anatolia and the North Caucasus) no longer exists. We further propose this fact to have recourse both to diverse source populations (especially in the case of mtDNA) and to demographic reorganization of peoples caused by feudal policies until relatively recent years. Since there is no evident phylogeographic patterning in Svaneti overall, we may provisionally conclude that patterns of diversity in Svaneti also reflect older demographic processes. A future comparative study of haplotype frequencies between Upper and Lower Svaneti, and Upper and Lower Bal, might elucidate this further, but additional sampling may be required.

VI.b Future Directions

The overall animating question of the Georgian Genetic History Project is whether or to what extent the Kartvelian-speaking population share lineages, and thus common ancestry, with each other and with proximate populations within Georgia (or rather, within its purview of breakaway regions), who do not speak Kartvelian languages. If the Svans, Abkhaz and Ossetes share a common ancestry—the three proximate populations in the study—and gene flow between Kartvelian-speaking and other Caucasus populations is restricted, how can these facts contribute to an enhanced understanding of the peopling of the Caucasus? These questions cannot be fully explored and answered until more samples from Georgia and eastern Turkey (i.e., the Laz) are collected and analyzed, which is one of the goals of our ongoing work.

The Georgia Genetic History Project is a multi-national collaborative project aimed at sampling broadly and deeper within Georgia. As with this dissertation project, our intention is to visit every village, town, and city in a target region, encouraging as many non-consanguineal individuals who wish to participate to do so. This approach will result in a better comparative understanding of Georgian and South Caucasus population history and the formation of identities in different regions. Had we not been both broad and deep in our sampling approach to this project, our understanding of mtDNA diversity in Svaneti would be limited.

Based on the findings of this dissertation project, the collaborative project will, pending financial support, undertake comparative studies in several regions of Georgia during the next three years. We hope to travel to Samegrelo (Mingrelia), Guria and

Ajara, and Samtskhe-Javakheti in 2015. The local governors of several of these regions are professional associates of Dr. Shengelia, and thus we anticipate being able to work with the help of local deputies and administrators, much as we did in Svaneti. In each location, the project details will be presented to community members. After obtaining informed consent, buccal swab samples as well as pertinent genealogical data will then be collected from participants in each region. We anticipate enrolling 80-100 individuals from villages and city districts in each region for a total of about 800 individuals overall. Through this strategy, samples from speakers of all four Kartvelian language families, as well as all participating non-Kartvelian minority populations, will be collected during a 3-5 year period.

The fruits of this project, combining data from multiple genetic systems (Y-chromosome, mtDNA, and possibly autosomal), and extensive ethnohistorical information, culled from interview and archival sources, will permit us to describe the genetic influences of multiple population events in the Caucasus and greater Near East. Once such events are identified, it should become possible to hypothesize broader cultural and genetic dynamics using new bio-quantitative tools (e.g., ALDER; see Loh et al. 2013; TREEMIX, see Pickrell and Pritchard 2012; Geographic Population Structure, see Elhaik et al. 2013; see also Hellenthal et al. 2014). Perhaps also the methods developed in this study of the Caucasus can be used to evaluate or re-evaluate populations living in similar isolated, highland, or ‘refuge’ areas.

APPENDICES

Appendix 1. Paleoclimatic and chronology chart for the SW and Southern Caucasus (Golovanova and Doronichev 2003)

GIS	Age (yr)	European climatic stages	Floristic characteristic	Climates		Southwestern Caucasus, Russia - Khosta Group	Southern Caucasus - Erevan-Taglar Group
2	20 000		Sub-alpine meadows	Cold, humid	Mabuzka (720 m)	Navali-shen-skaya (200 m)	
	30 000		Periglacial meadow-steppes & pine dominated woods	Cold, dry	layers 3A - 3C	Alshatskaya (900 m)	
3	40 000	Denskamp	Deciduous temperate woods	Warm, dry	layer 4A	Verintbovskaya (250 m)	Taglar (650 m)
			Meadow-steppes & mixed pine dominated woods	Cool, dry	layer 4B 34, 200±1, 410	layer 2 (2A)	
			Sub-alpine meadows & pine dominated woods	Cold, dry	layers 4C - 4D (C14)	layer 2 (2B)	
						layer 3 55: 680-480	
4	50 000	Hengelo				layer 4 (C14)	Dasha-lakhi (500 m)
		Meescheoid	Mixed coniferous fir dominated woods	Cool, humid		layer 5	layers 2, 3
		Glinde					layers 4a, 4b
							layers 5, 6
5	60 000	Dereel	Periglacial meadow-steppes & pine dominated woods	Cold, dry	layer 6		Erevan (900 m)
	70 000		Sub-alpine meadows	Cold, humid	layer 5A		layers 1 - 2
	80 000	Oddenade	Periglacial meadow-steppes & pine dominated woods	Cold, dry			layers 3 - 4
6a	80 000		Meadow-steppes & deciduous temp. woods	Warm, dry	layer 6B (upper level)		layers >47,800; >49,000 (C14)
	90 000		Meadow-steppes & deciduous temp. woods	Warm, dry	layer 6B (lower level)		layers 6, 2, 6, 7
6b	90 000		Periglacial meadow-steppes	Cool, dry	layer 6B (lower level)		
	100 000	Brorup	Meadow-steppes & deciduous temp. woods	Cool, dry	layer 6 (upper level)		
6c	100 000		Deciduous woods with exotics	Subtropical, humid	layer 6 (middle level)		
	110 000		Meadow-steppes & deciduous temp. woods	Cool, dry	layer 6 (lower level)		
6d	120 000	Eemian	Deciduous woods with many exotics	Tropical, humid	layer 7 (lower level)		
	130 000						

Appendix 2: Consent Form (Georgian)

ინფორმირებული თანხმობის ფორმა

კვლევითი პროექტის სახელწოდება: გენეტიკური ვარიაცია საქართველოში:
მასალები კავკასიის ისტორიისთვის

ოქმის ნომერი: 814693

სამეცნიერო ხელმძღვანელი: თეოდორ გ. შური, ფილოსოფიის დოქტორი,
პენსილვანიის უნივერსიტეტის ანთროპოლოგიის დეპარტამენტი,
325 University Museum, 3260 South Street, Philadelphia,
PA 19104-6398, (215) 573-7632; email: tgschurr@sas.upenn.edu

სამეცნიერო თანა-ხელმძღვანელი: არამ იარდუმიანი,
პენსილვანიის უნივერსიტეტის ანთროპოლოგიის დეპარტამენტი,
325 University Museum, 3260 South Street, Philadelphia,
PA 19104-6398; email: aram2@sas.upenn.edu

გიწვევთ, მონაწილეობა მიიღოთ კვლევაში, რომელსაც ატარებენ დოქტორი შური და ბატონი იარდუმიანი (პენსილვანიის უნივერსიტეტი) და მკვლევარები საქართველოდან, მათ შორის- დოქტორი ლია ბითაძე და დოქტორი დავით ჭითანავა (საქართველოს ისტორიისა და ეთნოლოგიის ინსტიტუტი) და დოქტორი რამაზ შენგელია (თბილისის სახელმწიფო სამედიცინო უნივერსიტეტი).

წინამდებარე თანხმობის ფორმა განმარტავს კვლევის დეტალებს. გთხოვთ, ყურადღებით გაეცნოთ მას. სურვილის შემთხვევაში, შეგიძლიათ, სხვას სთხოვოთ ამ ტექსტის თქვენთვის გაცნობა. თუ რამეს ვერ გაიგებთ, შეგიძლიათ, დამატებითი განმარტების მისაღებად დახმარება ერთ-ერთ მკვლევარს სთხოვოთ.

ჩვენ ვთხოვთ თქვენი თემის ლიდერებს, თანხმობა განეცხადებინათ კვლევაში მონაწილეობაზე. ვინაიდან მათ კვლევაში თავიანთ მონაწილეობაზე თანხმობა დაადასტურეს, თქვენ შეგიძლიათ, მონაწილეობა მიიღოთ ამ პროექტის განხორციელებაში.

ჩვენ თქვენ პირადი შეხვედრის დროს მოგაწვდით ინფორმაციას და დეტალურ განმარტებებს კვლევის შესახებ. თქვენ შეიტყობთ, თუ როგორ წარიმართება კვლევა, და რა შესაძლო რისკები, ზიანი და სარგებელი ახლავს

თან მის განხორციელებას. თქვენ შეგიძლიათ დაგვისვათ იმდენი შეკითხვა, რამდენსაც მოისურვებთ. ამ კვლევის შესახებ თქვენ შეგიძლიათ ინფორმაცია მიაწოდოთ თქვენი ოჯახის წევრებსა და მეგობრებს. მასში მონაწილეობაში მიიღებასთან დაკავშირებით საბოლოო გადაწყვეტილების მისაღებად თქვენ საკმარისი დრო გეძლევათ.

რა მიზნების ისახავს ეს კვლევა?

ჩვენ გვსურს, უფრო მეტი ინფორმაცია მოვიპოვოთ იმ მიგრაციული მარშრუტების შესახებ, რომლითაც ადრეული ეპოქის ადამიანები გადაადგილდებოდნენ დედამიწის ერთი ადგილიდან მეორე ადგილზე. ჩვენ ასევე გვინდა, დავადგინოთ ის დრო და პროცესი, როცა და რომლის მეშვეობითაც ეს ადამიანები შევიდნენ კავკასიის ტერიტორიაზე და დასახლდნენ იმ რეგიონში, სადაც ახლა საქართველოს რესპუბლიკა მდებარეობს. ჩვენ ასევე გვსურს შევიტყოთ, თუ როგორ დასახლდნენ ადამიანები ამ ტერიტორიაზე. კვლევის პროცესში ამ შეკითხვებს პასუხი ადამიანის დნმ-ს და გენეტიკური კოდების შესწავლით გაეცემა. დნმ-ს და გენეტიკური კოდების შესახებ ინფორმაციას ამ თანხმობის ფორმის მე-2 გვერდზე წარმოგიდგენთ. ის მკვლევარები, რომლებთან ერთადაც თქვენ მოგიწევთ მუშაობა, ასევე დეტალურ ინფორმაციას მოგაწვდიან დნმ-ს და გენეტიკური კოდების შესახებ. ჩვენ ვაპირებთ თქვენი საცხოვრებელი თემის მსგავსი, ანალოგიური თემების გამოკვლევას, სადაც ადამიანები ერთსა და იმავე ადგილზე ასეულობით და ათასობით წლის მანძილზე ცხოვრობენ.

რამდენი ადამიანი მიიღებს კვლევაში მონაწილეობას? რამდენ ხანს გაგრძელდება კვლევა?

ჩვენ ვვარაუდობთ, რომ კვლევაში მონაწილეობას მიიღებს დაახლოებით 3,500 ადამიანი საქართველოს შვიდი რეგიონიდან.

რისთვის ტარდება ეს კვლევა?

ამ კვლევის ფარგლებში ჩვენ ვგეგმავთ, პასუხი გავცეთ შემდეგ ძირითად შეკითხვებს:

- ა. მსოფლიოს რომელი კუთხიდან გამოვიდნენ თავდაპირველად ადამიანები ათასობით წლის წინ?
- ბ. თავიანთი თავდაპირველი საცხოვრებელი ადგილის დატოვების შემდეგ,

რა გზა განვლეს ადრეულმა ადამიანებმა დედამიწის ერთი ადგილიდან მეორეზე გადაადგილების პროცესში? როდის მოვიდნენ ისინი კავკასიაში?

გ. როგორ დასახლდნენ თქვენი საცხოვრებელი თემის მსგავსი ანალოგიური თემები დღევანდელ ტერიტორიაზე?

დ. როდის დაიწყო კავკასიაში ადამიანებმა თავიანთ მშობლიურ ენებზე მეტყველება?

როგორ გვეხმარება დნმ იმის გაგებაში, თუ როგორ გადაადგილდებოდნენ ადამიანები დედამიწაზე?

დნმ ადამიანის სხეულის ყველა უჯრედშია და მას სხვაგვარად ადამიანის გენეტიკურ კოდს უწოდებენ. თქვენი გენეტიკური კოდის მონაკვეთები შეიცავენ დნმ მარკერებს. ისინი ყოველ თაობაში მშობლიდან შვილს გადაეცემა.

პროექტის მკვლევარები მოახდენენ შედარებას, თუ რა საერთოა და რით განსხვავდება თქვენი დნმ-ს მარკერები კვლევაში მონაწილე სხვა ადამიანების მარკერებისგან. ეს მეცნიერებს უკეთეს წარმოდგენას შეუქმნის იმ მარშრუტების შესახებ, რომლითაც ადრეული ადამიანები დიდი ხნის წინ გადაადგილდებოდნენ. ის ასევე დაეხმარება მეცნიერებს, უკეთესად გაიგონ, სად დასახლდნენ ეს ადამიანები საბოლოოდ.

როგორ წარიმართება კვლევა? რა მოხდება კვლევის პროცესში?

ეს კვლევა ორი ნაწილისგან შედგება. ორივე ნაწილი ერთად დაახლოებით 30 წუთს წაგართმევთ. თუ თქვენ გამოთქვამთ სურვილს, მონაწილეობა მიიღოთ კვლევაში და ამის შესახებ თანხმობა განაცხადოთ, პროცესი შემდეგნაირად წარიმართება.

ნაწილი 1. ჩვენ დაგისვამთ შეკითხვებს თქვენი ოჯახის შესახებ

კვლევის პირველ ნაწილში, მკვლევარი გთხოვთ შემდეგი ინფორმაციის წარმოდგენას: თქვენი სახელი და გვარი, ასაკი, დაბადების ადგილი და ის ენა, რომელზეც თავდაპირველად ისწავლეთ მეტყველება ბავშვობაში. მკვლევარი

ასევე დაგისვამთ კითხვებს თქვენი დედის და მამის დაბადების ადგილების და პაპების და ბებიების შესახებ. ეს ინფორმაცია მეცნიერებს დაეხმარება, უკეთესი წარმოდგენა შეექმნათ თქვენს ისტორიასა და თქვენი დნმ-ს შესახებ.

თქვენ არავინ დაგისვამთ შეკითხვებს თქვენი ჯანმრთელობის, სამედიცინო ისტორიის ან დაავადებების შესახებ.

ნაწილი 2. ჩვენ ავიღებთ დნმ-ს სინჯს

თქვენი ოჯახის შესახებ შეკითხვების დასმის შემდეგ, ჩვენ ავიღებთ თქვენი დნმ-ს სინჯს ამ სამიდან ერთ-ერთი გზით:

1. ექიმი ან კვალიფიციური სამედიცინო მუშაკი თქვენს მკლავზე მდებარე ვენიდან აიღებს 2-3 სუფრის კოვზის მოცულობის სისხლს.
2. ლოყის შიდა მხარეზე, პლასტმასის საფხეკით, რომლის წვერზეც ქსოვილია გადაკრული, ავიღებენ ნაცხს. ეს ჩვენ თქვენი პირის ღრუდან დნმ-ს ნიმუშის აღების საშუალებას მოგვცემს.
3. ჩვენ ავიღებთ ნერწყვის სინჯს თქვენს მიერ პირში სპეციალური ხსნარის გამოვლევით და შემდეგ მისი კონტეინერში გადმოფურთხებით. მის შემადგენლობაში იქნება თქვენი დნმ-ს ნიმუში.

ამ კვლევის დროს არ მოხდება თქვენი დნმ-ს ტესტირება რაიმე დაავადების გამოსავლენად.

რა მოხდება მას შემდეგ, რაც დნმ-ს სინჯს აიღებენ?

ჩვენ თქვენს სინჯებს წავიღებთ პენსილვანიის უნივერსიტეტის ანთროპოლოგიის დეპარტამენტში, სადაც მეცნიერები შეისწავლიან თქვენს დნმ-ს ლაბორატორიული მეთოდებით და კომპიუტერული ანალიზის მეშვეობით. თქვენი დნმ-ს გენეტიკური კოდები შედარდება კვლევაში მონაწილე სხვა ადამიანების გენეტიკურ კოდებს.

სინჯების ლაბორატორიული ანალიზისას მთავარი აქცენტი გაკეთდება გენეტიკური მარკერების იდენტიფიცირებაზე, გენეალოგიური ურთიერთკავშირების დასადგენად. რაიმე სამედიცინო ხასიათის მარკერები არ იქნება გამოკვლეული- ჩვენი მიზანია თქვენი წინაპრების, თქვენი გვარის გენეტიკური კომპონენტების შეფასება და მათი ისტორიულ ეპოქაში არსებულ მიგრაციულ მოდელებთან ურთიერთმიმართების დადგენა. ის ორი მარკერი, რომლებიც უნდა გამოვლინდეს, გზდება მამისგან მემკვიდრეობით მიღებულ, მამაკაცების Y- ქრომოსომაზე, და დედის ხაზით მიღებულ მიტოქონდრიულ დნმ-ში მამაკაცებშიც და ქალებშიც. წინაპრების ისტორიის ანალიზის მიზნით ასევე შეიძლება დადგინდეს აუტოსომური (ორივე მშობლის მხრიდან გადმოცემული) მარკერები (რომლებსაც სამედიცინო დატვირთვა არ აქვთ).

შვიდწლიანი კვლევის განმავლობაში, დნმ-ს ყველა ნიმუში შეინახება პროექტის სამეცნიერო ხელმძღვანელის, დოქტორ შურის ლაბორატორიაში ამერიკაში. თქვენს მიერ ჩვენთვის მოწოდებული, დაფიქსირებული ნებისმიერი პირადი ინფორმაცია, ასევე თქვენს მიერ ხელმოწერილი თანხმობის ფორმა უსაფრთხო ადგილზე იქნება შენახული, ჩაკეტილ კაბინეტში, და ხელმისაწვდომი იქნება მხოლოდ კვლევითი გუნდის ამერიკელი და ქართველი წევრებისათვის.

ყველა პირს, რომლებიც სინჯებს ჩააბარებენ, მიენიჭებათ შემთხვევით შერჩეული ანბანურ-ციფრული საპროექტი კოდი, რათა მათი შედეგები პროექტის მონაცემთა ბაზაში ანონიმურად შეინახოს. ეს დაგვეხმარება კვლევის დროს მოპოვებული გენეტიკური ინფორმაციის შედარებითი ანალიზის განხორციელებაში.

ლაბორატორიული ანალიზის ჩატარების შემდეგ, გენეტიკური მონაცემები აიტვირთება დოქტორ შურის ლაბორატორიის მონაცემთა ბაზაში. მასში დაფიქსირდება თითოეული მონაწილის სქესი, ასაკი და ინფორმაცია წინაპრების შესახებ, თუმცა არ იქნება მითითებული არანაირი სამედიცინო ხასიათის ინფორმაცია. ამ ბაზის მეშვეობით ჩვენ შევძლებთ მონაწილეთა დნმ-ს გენეტიკური მარკერების შედარებას კავკასიაში, ახლო აღმოსავლეთსა და დანარჩენ მსოფლიოში მცხოვრები ადამიანების ანალოგიურ მარკერებთან.

თქვენი დნმ-ს სინჯი სხვა, გარეშე პირს არ გადაეცემა. დნმ-ს სინჯები პროექტის მიმდინარეობისას და მის შემდეგაც, არავითარ შემთხვევაში არ

გადაეცემა არავის, გარდა საქართველოს გენეტიკური ისტორიის პროექტზე მომუშავე პერსონალისა. ანალოგიურად, სინჯები და დნმ-ს სინჯები არ გაიყიდება, დაპატენტდება ან გარდაიქმნება უჯრედების კოლონიებად. მონაწილე მეცნიერებს ამ ნიმუშების კომერციალიზაციით არანაირი ფინანსური დაინტერესება არ გააჩნიათ.

რა შესაძლო რისკები, ზიანი ან დისკომფორტი ახლავს თან ამ კვლევას?

პირის ღრუდან ნაცხის აღება არანაირ რისკთან არაა დაკავშირებული, გარდა იმ მცირე დისკომფორტისა, რომელიც შეიძლება თან ახლდეს ნაცხის აღების პროცესს. ვენიდან სისხლის აღების დროს შეიძლება ადგილი ჰქონდეს სისხლდენას, ადგილობრივ სისხლჩაქცევას, ინფექციის წარმოქმნას და გულის წასვლას. ჯანმრთელ ადამიანებში ამგვარი ფაქტები ძალიან იშვიათად ხდება. ასევე შესაძლებელია, რომ კვლევის შედეგად მიღებული შედეგები განსხვავდებოდეს თქვენი თემის ზეპირი, წერილობითი ან სხვა სახის ტრადიციებისგან. ამან შესაძლოა გარკვეული გავლენა იქონიოს თქვენზე, თქვენს ოჯახზე და თქვენს თემზე. თუ ეს თქვენთვის სერიოზულ პრობლემას წარმოადგენს, შეგიძლიათ, კვლევაში მონაწილეობისგან თავი შეიკავოთ. მონაწილეობაზე თანხმობის თქმა მთლიანად თქვენს ნებაზეა დამოკიდებული.

შესაძლოა მომავალში გაჩნდეს ისეთი რისკები, რომლის შესახებაც კვლევისათვის ამჟამად არაფერია ცნობილი.

ზოგიერთი ადამიანი შეიძლება გარკვეულ დისკომფორტს განიცდიდეს მომავალში მოსალოდნელ შესაძლო სარგებელთან, რისკებთან თუ ზიანთან დაკავშირებით. თუკი კვლევის დროს ამგვარი ახალი სარგებლის, რისკების თუ ზიანის შესახებ ინფორმაციას მოვიპოვებთ, ამის შესახებ ჩვენ თქვენ აუცილებლად შეგატყობინებთ.

რა სარგებელს მოიტანს კვლევაში მონაწილეობა?

თქვენ შეიტყობთ ახალ ინფორმაციას იმის შესახებ, თუ რა ურთიერთობა გაქვთ თქვენ და თქვენს თემს მსოფლიოში მცხოვრებ დანარჩენ ადამიანებთან. თქვენ ასევე მიიღებთ ინფორმაციას თქვენი შორეული წინაპრების შესახებ. თქვენ შეიძლება გაიგოთ, თუ როგორ განვლეს მათ გრძელი გზა იმ

ადგილამდე, რომელსაც ახლა თქვენ საკუთარ სახლს უწოდებთ. თქვენ ყველა იმ პირად ინფორმაციასაც მიიღებთ, რომელიც კვლევის დროს ტესტირების პროცესში გამოვლინდება.

რა მოხდება, თუ მე არ მივიღებ მონაწილეობას კვლევაში?

არაფერი. თქვენ ნებისმიერ დროს შეგიძლიათ განაცხადოთ უარი და არ მიიღოთ კვლევაში მონაწილეობა.

კვლევაში მონაწილეობა ჩემთვის ფასიანი იქნება?

თქვენი დნმ-ს ნიმუშის აღება ან მისი შესწავლა თქვენთვის უფასოა, ისევე როგორც ჩვენი თქვენთან გასაუბრება თქვენი შედეგების გაცნობის მიზნით.

კვლევაში მონაწილეობისთვის ანაზღაურებას გადამიხდიან?

არა. კვლევის მონაწილეებს ფულს არ გადაუხდიან.

როგორ იქნება დაცული ჩემი დნმ-ს და ჩემი ოჯახის ისტორიის კონფიდენციალურობა კვლევის დროს?

თქვენი დნმ-ს სინჯს მიენიჭება პროექტის უნიკალური კოდი, რომელიც იქნება გამოყენებული თქვენი დნმ-ს ტესტის შედეგების განხილვისას. თქვენი სახელი სინჯზე არ იქნება აღნიშნული. პროექტის ეს კოდი, თქვენი თანხმობის ფორმის ასლი და თქვენი ოჯახის ისტორია (გენეალოგიური ფორმა) შეინახება პენსილვანიის უნივერსიტეტში, ჩაკეტილ საქაღალდეში. პროექტის ამ კოდით შესაძლებელი იქნება თქვენი დნმ-ს შესახებ ინფორმაციასა და თქვენ სახელსა და გვარს შორის კავშირის იდენტიფიცირება.

რა ბედი ელის ჩემს დნმ-ს კვლევის დასრულების შემდეგ?

კვლევის დასრულების შემდეგ, თქვენი დნმ-ს ნიმუში განადგურდება, იმ შემთხვევაში, თუ წინაპრებისა და ისტორიის შესახებ სამომავლო კვლევებისათვის მისი გამოყენების ნებას არ მოგვცემთ. ამ ფორმის ბოლოში, თქვენ შეგიძლიათ გაგვიზიაროთ თქვენი მოსაზრება ამ საკითხთან დაკავშირებით. პენსილვანიის უნივერსიტეტი იქნება დნმ-ს სინჯების

შემნახველი ცენტრალური ადგილი, კერძოდ- დოქტორ შურის ლაბორატორია, რომელშიც შეინახება დნმ-ს ყველა ნიმუში და მონაცემები პროექტის მიმდინარეობის პერიოდში.

გახსოვდეთ: სამართლებრივი თვალსაზრისით, თქვენი დნმ-ს სინჯი ყოველთვის თქვენ გეკუთვნით. ეს ნიშნავს შემდეგს: თქვენ ნებისმიერ დროს შეგიძლიათ გვთხოვოთ თქვენი დნმ-ს სინჯის და თქვენს შესახებ არსებული პირადი ინფორმაციის განადგურება.

- თქვენი დნმ-ს ნაწილი ან მასთან დაკავშირებული რაიმე ინფორმაცია არასოდეს გაიყიდება;
- ვერავინ განაცხადებს პრეტენზიას, თქვენი დნმ-ს გამოყენებით ფული იშოვოს;
- თქვენგან არავინ მოითხოვს ინფორმაციას თქვენი ჯანმრთელობის ან კონკრეტული დაავადებების ან სამედიცინო ისტორიის შესახებ;
- თქვენი გენეტიკური სინჯი არასოდეს იქნება გამოყენებული რაიმე სამედიცინო კვლევის ჩასატარებლად;
- ჩვენ მკაცრად დავიცავთ თქვენს მიერ ჩვენთვის მოცემული ინფორმაციის კონფიდენციალურობას.

კიდევ რას შეიტყობთ ამ კვლევიდან?

ამ პროექტის საერთო შედეგები ბევრ სხვადასხვა ადგილზე იქნება წარმოდგენილი. ადამიანები ამის შესახებ მთელი მსოფლიოს მასშტაბით შეიტყობენ სამეცნიერო ჟურნალებისა და გაზეთების მეშვეობით, ასევე ტელევიზიით, რადიოთი და ინტერნეტით. თქვენს თემში მცხოვრები ზოგიერთი ადამიანი ამ გაზეთებს და პროგრამებს სხვებზე ადრე ნახავს.

კვლევის დროს მოპოვებული ინფორმაციის წინასწარი ვერსიის პრეზენტაცია კვლავ მოხდება ან პირადად ან თემის შეკრებაზე, რათა მოხდეს მისი გადამოწმება, და იქ გამოთქმული გარკვეული მოსაზრებების საბოლოო ანგარიშის მომზადებისას სათანადო გააზრება და ასახვა. ყველა შედეგის პრეზენტაცია მოხდება თქვენს მხარეში, ჯგუფის შეკრებაზე. ინდივიდუალური ინფორმაციის მიწოდება არ მოხდება. ყველა მონაწილე თემს მიეცემა ამ კვლევის შესახებ ინფორმაციის გაზიარების (გაცემის)

რწმუნება. ამგვარი რწმუნება წარმოდგენილი იქნება ამ კვლევასთან დაკავშირებულ სხვადასხვა გამოცემებში, კერძოდ, ყოველი გამოცემის იმ ნაწილში, სადაც ტრადიციულად მაღლობას უხდიან სხვადასხვა პირებს და ორგანიზაციებს. თუ თემი არ მოისურვებს თავისი ვინაობის გამჟღავნებას, ის ფსევდონიმით იქნება მოხსენიებული.

როგორ მივიღებ ჩემს პირად მონაცემებს?

კვლევის მიმდინარეობისას, თქვენ კვლევითი ჯგუფის რომელიმე წევრი პირადად დაგელაპარაკებათ და გაგაცნობთ თქვენს პირად შედეგებს.

რა ბედი ელის იმ პირის სინჯს მისი გარდაცვალების შესახებ?

ასეთ შემთხვევაში, კვლევაში მონაწილე პირების მეურვე პირები ან ახლო ნათესავები გააკოტროლებენ ამ ნიმუშების ბედს. მათ შეუძლიათ ნება მოგვცენ, გავაგრძელოთ ამ ნიმუშების შენახვა და მათი ტესტირება, ანდა სურვილის შემთხვევაში, შეუძლიათ ითხოვონ მათი განადგურება.

ვის შეიძლება დავურეკო, თუ კვლევის დროს რაიმე პრობლემა ან შეკითხვა გამიჩნდება?

თქვენ შეგიძლიათ დაუკავშირდეთ დოქტორ თეოდორ შურს ნომერზე (810) 215-573-7632, ასევე დოქტორ რამაზ შენგელიას ნომერზე (599) 565660.

თუ მიგაჩნიათ, რომ კვლევაში მონაწილეობით თქვენ რაიმე ზიანი მოგადგათ, გთხოვთ, დაგვიკავშირდეთ შემდეგ მისამართზე:

პენსილვანიის უნივერსიტეტის ინსტიტუციური განხილვის საბჭო, 215-898-2614. ასევე შეგიძლიათ დაგვირეკოთ ნომერზე- (99532) 311766.

რა მოხდება იმ შემთხვევაში, თუ მე კვლევის დატოვებას გადავწყვეტ?

კვლევიდან გამოსვლა თქვენ ნებისმიერ დროს შეგიძლიათ. თქვენ უფლება გაქვთ, ნებისმიერ დროს თქვათ უარი დნმ-ს გენეტიკურ ტესტირებაზე. თქვენ შეგიძლიათ გვთხოვოთ თქვენი დნმ-ს ნიმუშის განადგურება. ეს თქვენი

უფლებათა, რომ ნებისმიერ დროს მოითხოვოთ თქვენი დნმ-ს ნიმუშის, ოჯახის შესახებ არსებული და ნებისმიერი სხვა ჩანაწერის განადგურება.

თუ კვლევის დატოვებას გადაწყვეტთ, დაურეკეთ თეოდორ შურს ნომერზე 1-215-573-7632. თქვენ ასევე შეგიძლიათ მას მისწეროთ მისამართზე:

Laboratory of Molecular Anthropology, University of Pennsylvania, 426 University Museum, 3260 South Street, Philadelphia, PA 19104-6398,

ან გაუგზავნოთ შეტყობინება ელ-ფოსტაზე: tgschurr@sas.upenn.edu. თქვენ დაგჭირდებათ მხოლოდ თქვენი სახელის და გვარის და სინჯის კოდის დასახელება.

ვის დაუკავშირდეს

თუ თქვენ გაგიჩნდათ კითხვები ამ კვლევასთან დაკავშირებულ თქვენს უფლებებზე ან დაცვაზე, დაგვიკავშირდით შემდეგი საკონტაქტო მისამართზე:

პენსილვანიის უნივერსიტეტის ინსტიტუციური განხილვის საბჭოს დირექტორი:

(810) 215-573-1206. ან დარეკეთ პენსილვანიის უნივერსიტეტის მარეგულირებელ საქმეთა აპარატში ნომერზე- (810) 215-898-0082. ასევე შეგიძლიათ დარეკოთ შემდეგ ნომერზე: (99532) 311766. თუ თქვენ გაქვთ შეკითხვები პროექტთან დაკავშირებით, დაურეკეთ დოქტორ თეოდორ შურს ნომერზე: (810) 215-573-7632.

მე მსურს ჩავაბარო დნმ-ს შემდეგი სინჯი (გთხოვთ, აღნიშნეთ):

___ სისხლის ნიმუში

___ პირის ღრუს ნაცხი

___ ნერწყვი (პირის ღრუში სითხის გამოვლებით)

მე მსურს, რომ ჩემი დნმ-ს სინჯი (აღნიშნეთ ჩამოთვლილი პუნქტებიდან ერთი):

___ შეინახოს კვლევის დასრულების შემდეგ, ამ კვლევასთან დაკავშირებული სამომავლო კვლევებისათვის (2025 წლამდე და მხოლოდ არასამედიცინო კვლევებისათვის)

___ განადგურდეს კვლევის დასრულების შემდეგ.

ამ გვერდზე ხელმოწერით თქვენ აცხადებთ, რომ აცნობიერებთ ამ კვლევის შესახებ ინფორმაციას და ასევე იმას, რომ თქვენს შეკითხვებზე დამაკმაყოფილებელი პასუხები მიიღეთ და თანახმა ხართ, მონაწილეობა მიიღოთ კვლევაში.

მონაწილის სახელი და გვარი
თარიღი

მონაწილის ხელმოწერა

იმ პირის სახელი და გვარი,
ვინც ხელმოწერას იღებს

თარიღი

იმ პირის ხელმოწერა,
ვინც მონაწილისგან ხელმოწერას
იღებს

Appendix 3: Consent Form (English)

Title: Genetic Variation in Georgia: Implications for the Prehistory of the Caucasus

Protocol Number: 814693

Principal Investigator: Dr. Theodore G. Schurr, Department of Anthropology, University of Pennsylvania, 325 University Museum, 3260 South Street, Philadelphia, PA 19104-6398, (215) 573-7632; email: tgschurr@sas.upenn.edu

Co-Principal Investigator: Mr. Aram Yardumian, Department of Anthropology, University of Pennsylvania, 325 University Museum, 3260 South Street, Philadelphia, PA 19104-6398; email: aram2@sas.upenn.edu

You are invited to join a research study led by Dr. Schurr and Mr. Yardumian at the University of Pennsylvania, and researchers from the Republic of Georgia, including Drs. Lia Bitadze and David Chitanava from the Institute of History and Ethnology, and Dr. Ramaz Shengelia from T’bilisi State Medical University.

This **consent form** explains the details of the study. Please read the form carefully. If you prefer, someone will read it to you. If you do not understand something, ask one of the researchers to explain it.

We have asked your community leaders for their approval to participate in the study. Because they approved the research study, you can choose to join the study.

We will talk to you about the study and explain everything about it. You will learn how the study works and its possible risks, harms and benefits. You can ask us as many questions as you like. You can talk over the study with your family or friends. Take your time to think about it.

What are the goals of this study?

We want to better understand the migration paths that early humans took as they moved from one place on earth to another place, including the time and process by which humans entered the Caucasus and settled the area that is now the Republic of Georgia. We also want to learn how people came to live where they do today. The study will do this by looking at a person’s DNA or genetic code. We will explain about DNA and genetic codes starting on page 2 of this consent form. The researchers whom you are working with will also explain about DNA and genetic codes in detail. We are studying communities like yours where people have lived in the same place for hundreds or thousands of years.

How many people will be part of this study? For how long will this study last?

We anticipate that about 3,500 people from seven regions in Georgia will participate in this study over the course of seven years.

Why is this study being done?

With this study we wish to investigate these basic questions:

- A. What part of the world did humans first come from thousands of years ago?
- B. After early humans left their original homes, what paths did they travel as they moved from one place on earth to another place? When did they arrive in the Caucasus?
- C. How did communities like yours come to live where they do today?
- D. When did people in the Caucasus begin speaking their native languages?

To answer these questions, scientists will use DNA testing. A DNA test is also called a genetic test.

Why is DNA helpful in finding out how people moved around the earth?

DNA is found inside every cell in the body. It is also known as your genetic code. Sections of your genetic code contain DNA markers. These markers are passed from parent to child in each generation.

The project researchers will compare where your DNA markers are the same and where they are different from those of other people in the study. This will give the scientists a better idea of the paths that people traveled a long time ago. It will also help scientists better understand where these people ended up living today.

How does the study work? What will happen during the study?

There are two parts to this study. Both parts together will take around 30 min of your time. If you choose to join the study and give your consent, then here is what will happen.

Part I: We will ask questions about your family

In first part of the study, the researcher will ask questions such as: Your name, your age, where you were born and the language you were taught as a child. The researcher will also ask where your mother and father were born and similar questions about your grandparents. This information will help the scientists better understand your history and the story in your DNA.

No one will ask any questions about your health, medical history or disease information.

Part II. We will collect a DNA sample

After we ask questions about your family, we will take a DNA sample in one of two ways:

1. The inside of your cheek will be brushed with a cloth-tipped plastic scraper. This lets us get a DNA sample from the inside of your cheek.
2. You will provide a saliva sample. You will put mouthwash in your mouth and move it around, then spit the mouthwash into a container. The DNA sample will be in the liquid you have spit out.

Your DNA will not be tested for any disease information during this study.

After I give my DNA sample, what happens to it?

We will take your sample to the University of Pennsylvania's Department of Anthropology where scientists will examine your DNA with laboratory methods and computer analysis. Your DNA genetic codes will be compared with other peoples' genetic codes in the study.

The laboratory analysis of the samples will focus on identifying genetic markers to infer genealogical relationships. No markers of known medical relevance will be investigated – our goal is to assess genetic components of your ancestry and to discern their relationship to historical migration patterns. Two sets of markers to be typed occur on the paternally inherited Y-chromosome of males, and the maternally inherited mitochondrial DNA (mtDNA) of both males and females. Autosomal markers (inherited from both parents) of no medical relevance may also be typed in order to analyze ancestry and migration history.

All DNA samples will be stored at the laboratory of the Dr. Schurr, the American Principal Investigator, during the length of the seven-year study. All recorded personal history information that you may provide to us, as well as this signed informed consent form, will be kept in a secure and locked cabinet accessible to only members of American and Georgian research teams. A portion of your DNA sample will also be kept at the T'bilisi State Medical University as a back-up source of DNA for this study of ancestry and migration.

All persons who provide samples will be assigned a randomly generated alphanumeric project code to make their results anonymous in the project database and assist in the collation of the genetic data generated in the study.

After the laboratory analysis, the genetic data will be uploaded to a database in the Schurr laboratory. Gender, age, and ancestry information will be maintained for each participant, but no medical information will be solicited or recorded. By maintaining this database, we can make comparisons of the genetic markers in participants' DNA with those of persons from the Caucasus, Near East and the rest of the world.

Your DNA sample will not be shared with anyone else. No DNAs will be given to anyone outside of the Georgia Genetic History Project, for any reason, over the duration

of the project, or beyond.

Likewise, no samples or DNAs will be sold, patented, or transformed into cell lines. The participating scientists will not seek any financial gain from the commercialization of these samples.

What are the risks, harms or discomforts that could happen because of the study?

There are no risks involved in giving a buccal swab aside from possibly minor discomfort from the swabbing process. The mouthwash has a mint strong flavor that may be unpleasant to some people, but is otherwise harmless to participants. It is also possible that some results from this study may be different from the oral, written, or other traditions of your community. This could affect you, your family and your community. If this is a serious worry for you, then you should not join the study. Choosing to join the study is up to you alone.

There could be risks in the future that the study does not know now.

Some people may worry about benefits, risks or harms that could happen in the future. We will let you know if we learn about new benefits, risks or harms during the study.

What are the benefits to joining this study?

You may learn new things about how you and your community relate to other people around the world. You may also learn about your ancestors far in the past. You may learn how they made the long journey to the place you now call home. You can see all your personal information from tests done in this study.

What happens if I do not join the study?

Nothing will happen. You can say ‘no’ at any time, and not join the study.

Will it cost me money to join the study?

There is no cost to have your DNA sample taken or to get it tested. There is also no cost for us to discuss your results with you.

Will I be paid if I join the study?

No. The study will not pay anyone money to participate in the study.

How will the study keep my DNA and family history information private?

Your DNA sample will be given a unique project code, and this project code will be used when discussing your DNA test results. Your name will not be placed on the sample.

This project code, a copy of this consent form, and your family history (genealogy form) will be kept in a locked file at the University of Pennsylvania. There will be a connection between your DNA information and your name because of the project code.

What happens to my DNA after the study is over?

Once the study is over, your DNA sample will be destroyed unless you allow us to keep it for future studies of ancestry and history. You will tell us which option that you want at the end of this form. If you let us to keep your sample for future use, we will ask for additional permission (another consent form) to conduct new studies with it.

The University of Pennsylvania will have a central storage place for the DNA samples. This is Dr. Schurr's laboratory, which will store all the DNA samples and data for the duration of the project. Back-up DNA samples will also be kept at T'bilisi State Medical University.

Remember: Legally, you always own your DNA sample. This means: You can tell us to destroy your DNA sample and your personal information at any time.

- **No portion of your DNA, or any information from it can ever be sold.**
- **No one can claim a right to your DNA to make money from it.**
- **No health or disease information or medical history will be asked of you**
- **Your genetic sample will *never* be used for any medical study.**
- **We will carefully protect the privacy of the information that you give us.**

Who else will learn about this study?

The overall results from this project will be presented in many places. People from all over the world will learn about it in science magazines and newspapers, and on television, the radio, and the Internet. Certain people in your community will see these papers and programs before anyone else does.

A summary of the information collected during the study will be presented again, either personally or in a community forum, for verification, and any suggestions at that time will be considered and incorporated into the final report. All results will be presented at a group forum in your area. No individual information will be shared. All participating communities will be credited for providing information for this study. Such credit will appear in the acknowledgment section of all publications resulting from this research. If a community does not wish to be identified, a pseudonym will be created and used.

How can I get my personal results?

During the study, someone will talk to you in person or by telephone about your results. We can also provide summaries of individual results for distribution to participants by email or regular mail.

What happens to someone's sample after they die?

After people who joined the study are deceased, their guardians or next of kin control what happens to their samples. They can let us keep the stored samples and continue the tests, or they can ask us to destroy the samples.

Who can I call if I have concerns or questions during the study?

You can call Dr. Theodore Schurr, at (00+1)+215-573-7632. You may also call Dr Ramaz Shengelia at (599) 565660.

If you think that you have been harmed by joining the study, then please call:

The University of Pennsylvania Institutional Review Board at (00+1)+215-898-2614. You may also phone Dr. Shengelia at Tbilisi State Medical University at (99532) 311766.

What happens if I want to quit the study?

You can quit the study at any time. You can say no to any more DNA genetic testing. You can tell us to destroy the DNA sample we have already taken. It is your right at any time to have your DNA sample, family information, and all records destroyed.

To quit the study, call Theodore Schurr at (00+1)+215-573-7632. You may also write to him at: Laboratory of Molecular Anthropology, University of Pennsylvania, 426 University Museum, 3260 South Street, Philadelphia, PA 19104-6398, or send an email to him at: tgschurr@sas.upenn.edu. All you have to do is give your name and sample code.

Who to call

If you have questions about your rights or protection in this study, call:

The Director of the Institutional Review Board at the University of Pennsylvania: (00+1)+215-573-1206. Or, call the University of Pennsylvania’s Office of Regulatory Affairs: (00+1)+215-898-0082. You may also phone Dr. Shengelia at T’bilisi State Medical University at (99532) 311766.

If you have questions about the project, call Dr. Theodore G. Schurr at (00+1)+215-573-7632.



I would like to provide the following DNA sample (please check):

- Check swab
- Saliva (mouthwash)

I would like my DNA sample to be (please check one):

- Destroyed when this study ends
- Stored after the study is finished for future studies related to the current research protocol (until the year 2020 and only for non-medical studies)

When you sign this page, you are saying that you understand this study. You are also saying that your questions have been answered to your satisfaction, and that you agree to join this study.

_____ Name of Participant	_____ Signature of Participant	_____ Date
_____ Name of Person Obtaining Signature	_____ Signature of Person Obtaining Signature	_____ Date

Appendix 4: Genealogy Form (Georgian)

გენეალოგიური კვლევის კითხვარი

პროექტი: გენეტიკური ვარიაცია საქართველოში: მასალები კავკასიის ისტორიისათვის

Principal Investigator: Dr. Theodore G. Schurr, Department of Anthropology, University of Pennsylvania, 426 University Museum, 3260 South Street, Philadelphia, PA 19104-6398;

Tel: (215) 573-7632; Email: tgschurr@sas.upenn.edu

Co-Principal Investigator: Aram Yardumian, Department of Anthropology, University of Pennsylvania, 325 University Museum, 3260 South Street, Philadelphia, PA 19104-6398;

Email: aram2@sas.upenn.edu

ინტერვიუერი: "თქვენთვის ცნობილია, რომ შეგიძლიათ არ უპასუხოს ნებისმიერ შეკითხვას და რომ შეგიძლიათ შეწყვიტოთ ინტერვიუ ნებისმიერ დროს? "

პასუხი : _____

ინტერვიუერი: "გსურთ გაგრძელება?"

პასუხი: _____

ინტერვიუერი: " ჩვენ ვიწყებთ ინტერვიუს."

მონაწილის სახელი _____ დაბადების თარიღი _____

სქესი _____ ენის ცოდნა _____

ეთნიკური წარმოშობა _____

თანამეგობრობის მონაწილე _____

დაბადების ადგილი _____

ინტერვიუს თარიღი _____ ინტერვიუს ადგილი _____

მშობელთა დედის სახელი _____

ენები, რომელთაც დედა ფლობს _____

დედის დაბადების ადგილი _____

დედის ეთნიკური წარმოშობა _____

მამის სახელი _____

ენები, რომელთაც მამა ფლობს _____

მამის დაბადების ადგილი _____

მამის ეთნიკური წარმოშობა _____

დედის ოჯახი

ბების სახელი (დედის დედა) _____

ენები, რომელთაც ბებია ფლობს _____

ბების დაბადების ადგილი _____

ბების ეთნიკური წარმოშობა _____

ბაბუს სახელი (დედა მამა) _____

ენები, რომელთაც ბაბუა ფლობს _____

ბაბუს დაბადების ადგილი _____

ბაბუს ეთნიკური წარმოშობა _____

მამის ოჯახი

ბების სახელი, გვარი (მამის დედა)

ენები, რომელთა ბებია ფლობს _____

ბების დაბადების ადგილი _____

ბების ეთნიკური წარმოშობა _____

ბაბუს სახელი, გვარი (მამის მამა) _____

ენები, რომელთაც ბაბუა ფლობს _____

ბაბუს დაბადების ადგილი _____

ბაბუს ეთნიკური წარმოშობა _____

საკონტაქტო ინფორმაცია

ელფოსტის მისამართი: _____@_____

საფოსტო მისამართი: _____

გირჩევნიათ კომუნიკაცია ელექტრონული ფოსტით/
რეგულარული ფოსტით?

თქვენი კომენტარი:

Appendix 5: Genealogy Form (English)

Project: Genetic Variation in Georgia: Implications for the Prehistory of the Caucasus

Principal Investigator: Dr. Theodore G. Schurr, Department of Anthropology, University of Pennsylvania, 426 University Museum, 3260 South Street, Philadelphia, PA 19104-6398;
Tel: (215) 573-7632; Email: tgschurr@sas.upenn.edu

Co-Principal Investigator: Aram Yardumian, Department of Anthropology, University of Pennsylvania, 325 University Museum, 3260 South Street, Philadelphia, PA 19104-6398;
Email: aram2@sas.upenn.edu

Interviewer: "Do you understand that you do not have to answer any questions that you do not want to, and that you can stop this interview at any time?"

Response: _____

Interviewer: "Would you like to continue?"

Response: _____

Interviewer: "OK, we will now begin the interview."

Participant's Name _____ Date of Birth _____

Sex _____ Language(s) Spoken _____

Ethnic Origin _____

Community of Participant _____

Participant Birthplace _____

Date of Interview _____ Location of Interview _____

Parents

Mother's Name _____

Mother's Language(s) _____

Mother's Birthplace _____

Mother's Ethnic Origin _____

Father's Name _____

Father's Language(s) _____

Father's Birthplace _____

Father's Ethnic Origin _____

Mother's Family

Maternal Grandmother's Name _____

Maternal Grandmother's Language(s) _____

Maternal Grandmother's Birthplace _____

Maternal Grandmother's Ethnic Origin _____

Maternal Grandfather's Name _____

Maternal Grandfather's Language(s) _____

Maternal Grandfather's Birthplace _____

Maternal Grandfather's Ethnic Origin _____

Father's Family

Paternal Grandmother's Name _____

Paternal Grandmother's Language(s) _____

Paternal Grandmother's Birthplace _____

Paternal Grandmother's Ethnic Origin _____

Paternal Grandfather's Name _____

Paternal Grandfather's Language(s) _____

Paternal Grandfather's Birthplace _____

Paternal Grandfather's Ethnic Origin _____

Contact Information

Email Address: _____ @ _____

Postal Address: _____

Do you prefer communication by email or regular mail? _____

Comments:

Investigator and Affiliation _____

Appendix 6. Complete HVS-I sequence data

#	Haplotype#	Sample ID	Local ID	Ethnicity	Home Village	Sample Location	Hg	HVS1 Sequence (16024-16569)
193	GEO001	KASV12193	SV193	Georgian	Zestaponi	Tbilisi	C	A16051G-T16093C-C16223T-C16234T-T16288C-T16298C-T16311C-C16327T
84	SVN001	KASV12084	SV084	Svan	Becho	Becho	C	C16223T-C16249C-T16298C-C16327T
3	SVN001	KASV12003	SV003	Svan	Laghami	Laghami	C	C16223T-T16249C-T16298C-C16327T
62	SVN001	KASV12062	SV062	Svan	Tskhumari	Tskhumari	C	C16223T-T16249C-T16298C-C16327T
65	SVN001	KASV12065	SV065	Svan	Tskhumari	Tskhumari	C	C16223T-T16249C-T16298C-C16327T
67	SVN001	KASV12067	SV067	Svan	Becho	Becho	C	C16223T-T16249C-T16298C-C16327T
75	SVN001	KASV12075	SV075	Svan	Becho	Becho	C	C16223T-T16249C-T16298C-C16327T
89	SVN001	KASV12089	SV089	Svan	Etseri	Etseri	C	C16223T-T16249C-T16298C-C16327T
34	SVN002	KASV12034	SV034	Svan	Gardabani	Mulakhi	D	C16223T-T16362C-G16526A
59	SVN002	KASV12059	SV059	Svan	Tskhumari	Tskhumari	D	C16223T-T16362C-G16526A
92	SVN002	KASV12092	SV092	Svan	Etseri	Etseri	D	C16223T-T16362C-G16526A
30	SVN004	KASV12030	SV030	Svan	Mulakhi	Mulakhi	H	A16235Gh
14	SVN005	KASV12014	SV014	Svan	Mulakhi	Mulakhi	H	A16309G

170	SVN009	KASV12170	SV170	Svan	Khaishi	Khaishi	H	C16067T-A16293T-C16355T
174	SVN009	KASV12174	SV174	Svan	Khaishi	Khaishi	H	C16067T-A16293T-C16355T
176	SVN009	KASV12176	SV176	Svan	Idliani	Idliani	H	C16067T-A16293T-C16355T
4	SVN006	KASV12004	SV004	Svan	Mulakhi	Laghami	H	C16067T-C16188T-C16355T
32	SVN008	KASV12032	SV032	Svan	Jamushi (?)	Mulakhi	H	C16067T-C16355T
114	SVN009	KASV12114	SV114	Svan	Mestia	Mestia	H	C16167T-A16293T-T16355C
74	SVN010	KASV12074	SV074	Svan	Becho	Becho	H	C16184T
124	SVN010	KASV12124	SV124	Svan	Lenjeri	Mestia	H	C16184T
6	SVN011	KASV12006	SV006	Svan	Laghami	Laghami	H	C16192T
121	SVN011	KASV12121	SV121	Svan	Mestia	Mestia	H	C16192T
131	SVN011	KASV12131	SV131	Svan	Mulakhi	Mestia	H	C16192T
132	SVN011	KASV12132	SV132	Svan	Etseri	Mestia	H	C16192T
144	SVN011	KASV12144	SV144	Svan	Latali	Latali	H	C16192T
180	SVN011	KASV12180	SV180	Svan	Idliani	Idliani	H	C16192T
183	SVN011	KASV12183	SV183	Svan	Idliani	Idliani	H	C16192T

38	SVN012	KASV12038	SV038	Svan	Gentsvishi (Gulripshi)	Ipari	H	C16192T-C16355T
109	SVN013	KASV12109	SV109	Svan	Mestia	Mestia	H	C16218T-C16328A
181	SVN014	KASV12181	SV181	Svan	Idliani	Idliani	H	C16287T
35	SVN015	KASV12035	SV035	Svan	Mulakhi	Mulakhi	H	C16354T
188	GEO002	KASV12188	SV188	Georgian	Mtskheta	Tbilisi	H	C16354T
46	SVN016	KASV12046	SV046	Svan	Lentekhi District	Ipari	H	CRS
24	SVN017	KASV12024	SV024	Svan	Mulakhi	Mulakhi	H	G16129A-A16316G
82	SVN017	KASV12082	SV082	Svan	Becho	Becho	H	G16129A-A16316G
96	SVN017	KASV12096	SV096	Svan	Etseri	Etseri	H	G16129A-A16316G
166	SVN018	KASV12166	SV166	Svan	Chuberi	Chuberi	H	G16129A-A16183C-T16189C-16193.1C- A16390Gh
37	SVN006	KASV12037	SV037	Svan	Ipari	Ipari	H	T16067C-C16188T-C16355T
31	SVN020	KASV12031	SV031	Svan	Mulakhi	Mulakhi	H	T16311C
69	SVN020	KASV12069	SV069	Svan	Becho	Becho	H	T16311C
99	SVN020	KASV12099	SV099	Svan	Etseri	Etseri	H	T16311C
130	SVN020	KASV12130	SV130	Svan	Mestia	Mestia	H	T16311C

135	SVN020	KASV12135	SV135	Svan	Latali	Latali	H	T16311C
150	SVN020	KASV12150	SV150	Svan	Chuberi	Chuberi	H	T16311C
157	SVN020	KASV12157	SV157	Svan	Chuberi	Chuberi	H	T16311C
175	SVN021	KASV12175	SV175	Svan	Khaishi	Khaishi	H27	T16093C-G16129A-T16189C-16193.1C-A16316G
178	SVN023	KASV12178	SV178	Svan	Idliani	Idliani	I1a	G16129A-C16223T-T16311C-G16391A
158	SVN024	KASV12158	SV158	Svan	Chuberi	Chuberi	I1a	G16129A-T16172C-C16223T-T16311C-A16391A
177	SVN022	KASV12177	SV177	Svan	Idliani	Idliani	I1c	G16129A-C16218T-C16223T-C16264T-C16270T-T16311C-G16319A-T16362C-G16390A
194	GEO003	KASV12194	SV194	Georgian	Khashuri	Tbilisi	J	C16069T-T16126C-C16169T-C16193T-G16274A
103	SVN026	KASV12103	SV103	Svan	Etseri	Etseri	J	C16069T-T16126C-C16218T
197	GEO004	KASV12197	SV197	Georgian	Tbilisi	Tbilisi	J	C16069T-T16126C-G16129A-A16300G
52	SVN028	KASV12052	SV052	Svan	Ushguli	Ushguli	K	C16167T-T16224C-T16311C
107	SVN028	KASV12107	SV107	Svan	Mestia	Mestia	K	C16167T-T16224C-T16311C
126	SVN028	KASV12126	SV126	Svan	Mestia	Mestia	K	C16167T-T16224C-T16311C
140	SVN028	KASV12140	SV140	Svan	Latali	Latali	K	C16167T-T16224C-T16311C
147	SVN028	KASV12147	SV147	Svan	Latali	Latali	K	C16167T-T16224C-T16311C

29	SVN029	KASV12029	SV029	Svan	Mulakhi	Mulakhi	K	C16167T-T16224C-T16311C-T16359C
93	SVN029	KASV12093	SV093	Svan	Etseri	Etseri	K	C16167T-T16224C-T16311C-T16359C
18	SVN030	KASV12018	SV018	Svan	Mulakhi	Mulakhi	K	C16168T-T16224T-T16311C-T16359C
19	SVN030	KASV12019	SV019	Svan	Mulakhi	Mulakhi	K	C16168T-T16224T-T16311C-T16359C
53	SVN031	KASV12053	SV053	Svan	Ushguli	Ushguli	K	G16145A-T16224C-T16311C-A16497G
28	SVN032	KASV12028	SV028	Svan	Mulakhi	Mulakhi	K	T16093C-T16224C
41	SVN033	KASV12041	SV041	Svan	Ipari	Ipari	K	T16093C-T16224C-C16260T-T16311C
143	SVN033	KASV12143	SV143	Svan	Latali	Latali	K	T16093C-T16224C-C16260T-T16311C
2	SVN034	KASV12002	SV003	Svan	Laghami	Laghami	K	T16093C-T16224C-T16311C
7	SVN034	KASV12007	SV007	Svan	Mestia	Mestia	K	T16093C-T16224C-T16311C
10	SVN034	KASV12010	SV010	Svan	Mulakhi	Mulakhi	K	T16093C-T16224C-T16311C
66	SVN034	KASV12066	SV066	Svan	Tskhumari	Tskhumari	K	T16093C-T16224C-T16311C
134	SVN034	KASV12134	SV134	Svan	Latali	Latali	K	T16093C-T16224C-T16311C
167	SVN034	KASV12167	SV167	Svan	Khaishi	Khaishi	K	T16093C-T16224C-T16311C
169	SVN034	KASV12169	SV169	Svan	Khaishi	Khaishi	K	T16093C-T16224C-T16311C

182	SVN034	KASV12182	SV182	Svan	Idliani	Idliani	K	T16093C-T16224C-T16311C
185	SVN034	KASV12185	SV185	Svan	Idliani	Idliani	K	T16093C-T16224C-T16311C
192	GEO005	KASV12192	SV192	Georgian	Tbilisi	Tbilisi	K	T16093C-T16224C-T16311C
101	SVN035	KASV12101	SV101	Svan	Etseri	Etseri	K	T16093C-T16224C-T16311C-T16362C
76	SVN036	KASV12076	SV076	Svan	Becho	Becho	K	T16224C-A16246T-T16311C
120	SVN037	KASV12120	SV120	Svan	Mestia	Mestia	K	T16224C-T16311C
137	SVN037	KASV12137	SV137	Svan	Latali	Latali	K	T16224C-T16311C
165	SVN037	KASV12165	SV165	Svan	Chuberi	Chuberi	K	T16224C-T16311C
190	GEO006	KASV12190	SV190	Georgian	Poti	N/A	K	T16224C-T16311C
11	SVN037	KASV12011	SV011	Svan	Mulakhi	Mulakhi	K	T16224C-T16311C-A16497G
51	SVN037	KASV12051	SV051	Svan	Ushguli	Ushguli	K	T16224C-T16311C-A16497G
54	SVN039	KASV12054	SV054	Svan	Tskhumari	Tskhumari	M	C16223T-T16390A
94	SVN040	KASV12094	SV094	Svan	Etseri	Etseri	M1	G16129A-A16183C-T16189C-T16224C-T16249C-T16288C-C16295T
21	SVN041	KASV12021	SV021	Svan	?	Mulakhi	N1b 1	G16145A-C16176G-C16223T-G16390A
122	SVN041	KASV12122	SV122	Svan	Zugdidi	Mestia	N1b 1	G16145A-C16176G-C16223T-G16390A

148	SVN042	KASV12148	SV148	Svan	Latali	Latali	ROa 1a	C16071T-G16129A-C16355T-T16357C
13	SVN043	KASV12013	SV013	Svan	Mestia	Mulakhi	T	T16126C-C16294T
25	SVN043	KASV12025	SV025	Svan	Mulakhi	Mulakhi	T	T16126C-C16294T
63	SVN043	KASV12063	SV063	Svan	Tskhumari	Tskhumari	T	T16126C-C16294T
81	SVN043	KASV12081	SV081	Svan	Becho	Becho	T	T16126C-C16294T
129	SVN043	KASV12129	SV129	Svan	Lenjeri	Mestia	T	T16126C-C16294T
145	SVN043	KASV12145	SV145	Svan	Latali	Latali	T	T16126C-C16294T
106	SVN044	KASV12106	SV106	Svan	Mestia	Mestia	T1	T16126C-A16163G-C16185T-T16189C- T16249C
186	GEO009	KASV12186	SV186	Georgian	Tbilisi	N/A	T1	T16126C-A16163G-C16186T-T16189C- C16294T-C16294T
198	GEO007	KASV12198	SV198	Georgian	Tbilisi	Tbilisi	T1	T16126C-A16163G-C16186T-T16189C- C16294T-C16296T
200	GEO007	KASV12200	SV200	Georgian	Tbilisi	Tbilisi	T1	T16126C-A16163G-C16186T-T16189C- C16294T-C16296T
142	SVN045	KASV12142	SV142	Svan	Zugdidi	Latali	T1	T16126C-A16163G-C16186T-T16189C- T16209C-C16294T-G16390A
168	SVN046	KASV12168	SV168	Svan	Khashuri	?	T2	T16126C-A16163G-C16186T-T16189C- C16294T-C16296T
15	SVN047	KASV12015	SV015	Svan	Mestia	Mulakhi	T2	T16126C-C16223T-C16294T-C16296T
1	SVN092	KASV12001	SV001	Svan	Laghami	Laghami	T2	T16126C-C16270A-C16294T-C16296T

48	SVN092	KASV12048	SV048	Svan	Kala	Kala	T2	T16126C-C16270A-C16294T-C16296T
73	SVN048	KASV12073	SV073	Svan	Becho	Becho	T2	T16126C-C16294T-C16296T
20	SVN048	KASV12020	SV020	Svan	Chvabiani	Mulakhi	T2	T16126C-C16294T-C16296T
64	SVN048	KASV12064	SV064	Svan	Tskhumari	Tskhumari	T2	T16126C-C16294T-C16296T
113	SVN048	KASV12113	SV113	Svan	Mestia	Mestia	T2	T16126C-C16294T-C16296T
36	SVN049	KASV12036	SV036	Svan	Ipari	Ipari	T2	T16126C-G16153A-C16294T-C16296T
85	SVN050	KASV12085	SV085	Svan	Becho	Becho	U	C16295T-C16296T
87	SVN051	KASV12087	SV087	Svan	Becho	Becho	U	T16304C
77	SVN020	KASV12077	SV077	Svan	Becho	Becho	U	T16311C
5	SVN053	KASV12005	SV005	Svan	Laghami	Laghami	U1	C16111T-C16214A-T16249C-C16290T-C16327T
8	SVN053	KASV12008	SV008	Svan	Khaishi	Mestia	U1	C16111T-C16214A-T16249C-C16290T-C16327T
104	SVN053	KASV12104	SV104	Svan	Etseri	Etseri	U1	C16111T-C16214A-T16249C-C16290T-C16327T
112	SVN053	KASV12112	SV112	Svan	Mestia	Mestia	U1	C16111T-C16214A-T16249C-C16290T-C16327T
164	SVN053	KASV12164	SV164	Svan	Chuberi	Chuberi	U1	C16111T-C16214A-T16249C-C16290T-C16327T
163	SVN054	KASV12163	SV163	Svan	Chuberi	Chuberi	U1	C16111T-C16214A-T16249C-T16271C-C16290T-C16327T

90	SVN056	KASV12090	SV090	Svan	Etseri	Etseri	U1	C16111T-T16249C-C16327T
155	SVN056	KASV12155	SV155	Svan	Chuberi	Chuberi	U1	C16111T-T16249C-C16327T
171	SVN056	KASV12171	SV171	Svan	Khaishi	Khaishi	U1	C16111T-T16249C-C16327T
119	SVN040	KASV12119	SV119	Svan	Etseri	Mestia	U1	C16129A-A16183C-T16189C-T16224C-T16249C-T16288C-C16295T-C16527T
70	SVN058	KASV12070	SV070	Svan	Becho	Becho	U1	C16214A-T16249C-C16290T-C16327T
9	SVN059	KASV12009	SV009	Svan	Mulakhi	Mulakhi	U1	G16129A-A16183C-T16189C-T16249C-T16288C-C16295T-C16527T
22	SVN060	KASV12022	SV022	Svan	Mulakhi	Mulakhi	U1	A16183C-T16189C-C16223T-T16249C-G16390A
151	SVN061	KASV12151	SV151	Svan	Chuberi	Chuberi	U1	A16183C-T16189C-T16249C-G16390A
195	GEO010	KASV12195	SV195	Georgian	Akhmeta	Tbilisi	U1	16166Ad-A16182C-A16183C-T16189C-T16249C-T16311C
196	GEO011	KASV12196	SV196	Georgian	Tbilisi	Tbilisi	U2	A16051G-G16129C-C16147T-A16182C-A16183C-T16189C-C16256T-T16362C
45	SVN062	KASV12045	SV045	Svan	Kala	Ipari	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T
56	SVN062	KASV12056	SV056	Svan	Tskhumari	Tskhumari	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T
61	SVN062	KASV12061	SV061	Svan	Tskhumari	Tskhumari	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T
102	SVN062	KASV12102	SV102	Svan	Etseri	Etseri	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T

153	SVN062	KASV12153	SV153	Svan	Chuberi	Chuberi	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T
154	SVN062	KASV12154	SV154	Svan	Chuberi	Chuberi	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T
187	GEO012	KASV12187	SV187	Georgian	Tbilisi	Tbilisi	U2	A16051G-A16183C-T16189C-16193.1C-C16234T-C16294T
156	SVN062	KASV12156	SV156	Svan	Chuberi	Chuberi	U2	A16051G-A16183C-T16189C-16913.1C-T16234T-C16294T
125	SVN062	KASV12125	SV125	Svan	Mestia	Mestia	U2	A16051G-A16183C-T16189C-T16234T-C16294T
136	SVN062	KASV12136	SV136	Svan	Latali	Latali	U2	A16051G-A16183C-T16189C-T16234T-C16294T
78	SVN064	KASV12078	SV078	Svan	Becho	Becho	U2	C16234T-C16294T
79	SVN065	KASV12079	SV079	Svan	Becho	Becho	U2	C16294T
108	SVN066	KASV12108	SV108	Svan	Mestia	Mestia	U3	A16343G
127	SVN066	KASV12127	SV127	Svan	Mestia	Mestia	U3	A16343G
26	SVN068	KASV12026	SV026	Svan	Mulakhi	Mulakhi	U3	A16183C-T16189C-T16217C-A16343G-G16390A
199	GEO013	KASV12199	SV199	Georgian	Tbilisi	Tbilisi	U3	A16183C-T16189C-T16217C-A16343G-G16390A
16	SVN067	KASV12016	SV016	Svan	Mestia	Mulakhi	U3	T16189C-T16325C-A16343G-G16390A-T16406C
159	SVN071	KASV12159	SV159	Svan	Chuberi	Chuberi	U4	G16213A-T16356C-T16424C-G16438A

33	SVN073	KASV12033	SV033	Svan	Mestia	Mulakhi	U4	T16356C
39	SVN073	KASV12039	SV039	Svan	Ipari	Ipari	U4	T16356C
47	SVN073	KASV12047	SV047	Svan	Ipari	Ipari	U4	T16356C
133	SVN071	KASV12133	SV133	Svan	Tbilisi	Latali	U5	G16213A-T16356C-T16422C
118	SVN072	KASV12118	SV118	Svan	Mestia	Mestia	U5	T16086C-T16356C
12	SVN073	KASV12012	SV012	Svan	Mestia	Mulakhi	U5	T16356C
128	SVN073	KASV12128	SV128	Svan	Mestia	Mestia	U5	T16356C
184	GEO014	KASV12184	SV184	Georgian	Tbilisi	N/A	U5	T16356C
161	SVN074	KASV12161	SV161	Svan	Chuberi	Chuberi	U5a	C16192T-C16256T-C16270T-T16311C-A16399G
91	SVN042	KASV12091	SV091	Svan	Etseri	Etseri	U6	C16071T-G16129A-C16355T-T16357C
71	SVN076	KASV12071	SV071	Svan	Becho	Becho	U6	C16355T-T16357C
72	SVN077	KASV12072	SV072	Svan	Becho	Becho	U6	G16129A-C16355T-T16357C
191	GEO015	KASV12191	SV191	Georgian	Tbilisi	Tbilisi	U7	A16309G-A16318T
179	SVN078	KASV12179	SV179	Svan	Idliani	Idliani	U7	A16318T-G16319A
17	SVN079	KASV12017	SV017	Svan	Mulakhi	Mulakhi	U7	C16223T-C16250T-C16256T-A16318T-T16368C

23	SVN080	KASV12023	SV023	Svan	Kala	Kala	U7a	T16126C-C16158T-T16209C-A16309G-A16318T-G16390A
57	SVN081	KASV12057	SV057	Svan	Tskhumari	Tskhumari	W6	A16164G-C16192T-C16223T-C16292T-T16325C
55	SVN088	KASV12055	SV055	Svan	Tskhumari	Tskhumari	W	C16223T-C16292T
42	SVN089	KASV12042	SV042	Svan	Ipari	Ipari	W	C16292T
60	SVN081	KASV12060	SV060	Svan	Tskhumari	Tskhumari	W6	A16164G-C16192T-C16223T-C16292T-T16325C
97	SVN081	KASV12097	SV097	Svan	Etseri	Etseri	W6	A16164G-C16192T-C16223T-C16292T-T16325C
152	SVN081	KASV12152	SV152	Svan	Chuberi	Chuberi	W6	A16164G-C16192T-C16223T-C16292T-T16325C
110	SVN083	KASV12110	SV110	Svan	Mestia	Mestia	W6	C16188T-T16189C-C16223T-C16292T-T16325C-T16445C
111	SVN084	KASV12111	SV111	Svan	Mestia	Mestia	W6	C16188T-T16189C-C16223T-T16325C-T16445C
100	SVN085	KASV12100	SV100	Svan	Etseri	Etseri	W6	C16192T-C16223T-C16278T-C16292T-T16325C
117	SVN085	KASV12117	SV117	Svan	Mestia	Mestia	W6	C16192T-C16223T-C16278T-C16292T-T16325C
123	SVN085	KASV12123	SV123	Svan	Lenjeri	Mestia	W6	C16192T-C16223T-C16278T-C16292T-T16325C
83	SVN086	KASV12083	SV083	Svan	Becho	Becho	W6	C16192T-C16223T-C16292T-C16325C
88	SVN086	KASV12088	SV088	Svan	Becho	Becho	W6	C16192T-C16223T-C16292T-C16325C

116	SVN086	KASV12116	SV116	Svan	Mestia	Mestia	W6	C16192T-C16223T-C16292T-C16325C
43	SVN086	KASV12043	SV043	Svan	Ipari	Ipari	W6	C16192T-C16223T-C16292T-T16325C
80	SVN086	KASV12080	SV080	Svan	Becho	Becho	W6	C16192T-C16223T-C16292T-T16325C
86	SVN086	KASV12086	SV086	Svan	Becho	Becho	W6	C16192T-C16223T-C16292T-T16325C
138	SVN086	KASV12138	SV138	Svan	Latali	Latali	W6	C16192T-C16223T-C16292T-T16325C
139	SVN086	KASV12139	SV139	Svan	Latali	Latali	W6	C16192T-C16223T-C16292T-T16325C
146	SVN086	KASV12146	SV146	Svan	Latali	Latali	W6	C16192T-C16223T-C16292T-T16325C
149	SVN086	KASV12149	SV149	Svan	Latali	Latali	W6	C16192T-C16223T-C16292T-T16325C
68	SVN086	KASV12068	SV068	Svan	Becho	Becho	W6	C16192T-C16223T-C16292T-T16325C-G16504A
172	SVN090	KASV12172	SV172	Svan	Khaishi	Khaishi	W6	T16189C-C16192T-C16223T-C16292T-C16295T-A16322G-T16325C
141	SVN091	KASV12141	SV141	Svan	Latali	Latali	W6	C16223T-T16325C-T16445C
189	GEO016	KASV12189	SV189	Georgian	Tbilisi	Tbilisi	W6	C16223T-T16325C-T16445C
98	SVN095	KASV12098	SV098	Svan	Etseri	Etseri	X2	C16104T-T16189C-C16223T-C16278T
162	SVN096	KASV12162	SV162	Svan	Chuberi	Chuberi	X2	C16192T-A16182C-A16183C-T16189C-C16223T-C16278T
95	SVN103	KASV12095	SV095	Svan	Etseri	Etseri	X2	G16129A-T16140C-A16183C-T16189C-C16223T-C16278T

105	SVN097	KASV12105	SV105	Svan	Mestia	Mestia	X2	G16129A-A16182C-A16183C-T16189C-C16223T-C16278T
40	SVN097	KASV12040	SV040	Svan	Ipari	Ipari	X2	G16129A-A16182C-A16183C-T16189C-16194.2C-C16223T-C16278T
44	SVN097	KASV12044	SV044	Svan	Ipari	Ipari	X2	G16129A-A16182C-A16183C-T16189C-16194.2C-C16223T-C16278T
27	SVN099	KASV12027	SV027	Svan	Tbilisi	Mulakhi	X2	A16183C-T16189C-16192.1C-C16223T-C16266T-C16278T-C16301T
115	SVN094	KASV12115	SV115	Svan	Mestia	Mestia	X2	A16182C-A16183C-T16189C-C16223T-C16278T
58	SVN100	KASV12058	SV058	Svan	Tskhumari	Tskhumari	X2	T16189C-C16223T-C16278T-A16316G
49	SVN102	KASV12049	SV049	Svan	Ushguli	Ushguli	X2	A16183C-T16189C-16193.1C-C16223T-C16278T-T16311C
50	SVN102	KASV12050	SV050	Svan	Ushguli	Ushguli	X2	A16183C-T16189C-16193.1C-C16223T-C16278T-T16311C
160	SVN102	KASV12160	SV160	Svan	Chuberi	Chuberi	X2	A16183C-T16189C-16193.1C-C16223T-C16278T-T16311C
173	SVN101	KASV12173	SV173	Svan	Khaishi	Khaishi	X4	A16182C-A16183C-T16189C-C16223T-G16256A-C16266T-G16274A-C16278T-T16304C-G16390A

Appendix 7. Population Pairwise F_{ST} data for Svan Settlement mtDNA (Significance level = 0.05)

	Becho	Chuberi	Etseri	Idliani	Ipari	Kala	Khaishi	Laghami	Latali	Lenjeri	Mestia	Mulakhi	Tshkumari	Ushguli
Becho	0	-	-	-	-	+	-	-	-	-	-	+	-	+
Chuberi	0.043	0	-	-	-	-	-	-	+	-	-	-	-	-
Etseri	0.006	-0.014	0	-	-	+	-	-	-	-	-	-	-	-
Idliani	0.024	0.042	0.009	0	-	+	-	-	-	-	-	-	-	-
Ipari	0.007	0.006	-0.018	-0.011	0	+	-	-	-	-	-	-	-	+
Kala	0.179	0.087	0.12	0.162	0.099	0	-	-	-	-	-	+	-	+
Khaishi	0.042	-0.008	-0.023	-0.01	-0.022	0.093	0	-	-	-	-	-	-	-
Laghami	-0.025	-0.024	-0.042	0.016	0.006	0.027	-0.062	0	-	-	-	-	-	+
Latali	0.016	0.055	0.019	-0.03	0.013	0.204	0.039	0.043	0	-	-	-	-	-
Lenjeri	-0.101	-0.019	-0.07	-0.054	-0.122	-0.034	-0.048	-0.074	-0.064	0	-	-	-	-
Mestia	0.013	0.009	0.005	0.024	-0.037	0.114	0.012	0.002	0.014	-0.079	0	-	-	+
Mulakhi	0.046	0.027	0.01	0.023	0.01	0.123	0.014	0.008	0.033	-0.004	0.002	0	+	+
Tshkumari	-0.011	0.027	-0.003	0.035	-0.006	0.128	0.032	-0.006	0.036	-0.101	0.008	0.057	0	+
Ushguli	0.217	0.084	0.086	0.086	0.133	0.331	0.080	0.172	0.106	0.24	0.119	0.095	0.186	0

Appendix 8. Complete Svan Y-STR haplotype data

Raw Data Consolidated ID #s	N	Hg	Svan NRY STR Haplotypes																			
			Haplotype ID #s																			
SV001	1	R1a	19	3851	385II	389I	389II	390	391	392	393	437	438	439	448	456	458	635	H4			
SV002	2	G2a	16	11	15	13	30	25	11	11	13	14	11	10	20	16	16	23	12			
SV003	2	G2a	15	15	18	12	28	22	10	10	14	16	8	11	21	15	16	21	11			
SV004	4	G2a	15	15	16	12	29	22	10	10	14	16	10	11	21	17	17	21	12			
SV005	1	G2a	15	15	16	12	29	22	10	10	14	16	10	11	21	16	18	21	11			
SV006	1	I2a	16	15	16	12	27	22	9	10	14	14	10	13	21	16	17	21	12			
SV007	1	G2a	17	12	13	13	31	24	10	11	13	15	11	13	20	15	18	21	11			
SV008	1	I2a	15	14	16	12	28	22	10	10	14	16	10	10	21	15	17	21	11			
SV009	1	R1a	16	12	13	13	30	24	10	11	14	15	10	12	20	15	18	21	11			
SV010	1	G2a	16	12	14	13	30	25	11	11	13	14	11	10	19	17	15	23	12			
SV011	1	G2a	15	14	16	13	30	22	10	10	14	16	11	11	21	16	17	21	11			
SV012	1	G2a	15	15	17	11	29	22	10	10	14	15	10	12	21	15	16	21	11			
SV013	1	I2a	15	14	16	12	29	22	10	10	14	16	11	11	21	16	17	21	11			
SV014	2	G2a	14	14	17	13	29	24	10	11	12	15	9	12	20	14	18	21	11			
SV015	1	G2a	15	15	16	12	29	22	10	10	14	16	10	11	21	15	18	21	11			
SV016	1	G2a	15	15	17	12	29	22	10	10	14	16	10	11	21	16	17	21	11			
SV017	1	G2a	15	15	17	12	29	22	10	10	14	16	10	11	21	16	17	21	11			
SV018	1	N	15	15	17	12	29	22	10	10	14	16	10	11	21	15	16	21	12			
SV019	1	G2a	15	14	16	13	30	22	10	10	14	16	10	11	21	16	17	21	11			
SV020	1	R1a	14	11	14	14	30	23	10	14	13	14	10	10	20	14	17	21	12			
SV021	1	I2a	15	15	14	14	12	29	23	10	11	14	16	10	12	16	18	21	12			
			16	12	14	13	31	25	10	11	14	14	11	10	20	15	16	23	13			
			15	13	13	13	30	24	10	11	14	14	10	11	19	15	17	21	11			

SY022	1	G2a	SV061	15	16	16	12	29	22	11	10	14	16	10	11	21	15	16	21	11
SY023	2	G2a	SV065, SV092	15	15	16	12	29	22	10	10	14	16	10	11	21	16	17	21	11
SY024	2	G2a	SV066, SV089	15	16	16	12	28	24	10	10	14	15	10	11	21	16	17	21	11
SY025	1	G2a	SV068	15	15	16	12	28	22	10	10	14	16	10	11	21	16	18	22	11
SY026	1	G2a	SV072	15	15	17	11	29	22	11	10	14	16	10	13	22	15	16	21	11
SY027	1	G2a	SV075	15	15	17	11	29	22	11	10	14	14	10	12	21	15	17	21	11
SY028	1	G2a	SV077	15	15	16	12	29	22	10	10	14	16	10	11	22	15	17	21	11
SY029	1	R1a	SV079	17	11	14	13	31	24	11	11	13	14	11	10	20	16	17	23	12
SY030	1	J2a1	SV080	15	15	17	14	30	23	10	11	12	14	9	12	20	15	17	22	11
SY031	2	G2a	SV081, SV100	15	15	17	12	29	22	10	10	14	16	10	12	21	15	15	22	11
SY032	1	G2a	SV083	15	15	16	12	28	24	10	10	14	16	10	11	21	15	17	20	11
SY033	1	J2a1	SV084	14	12	15	14	31	23	10	11	12	15	9	12	20	16	17	24	9
SY034	1	G2a	SV086	15	15	17	11	28	22	11	10	14	16	10	12	21	15	16	21	11
SY035	1	R1a	SV087	16	11	14	13	30	25	11	11	13	14	11	10	19	18	15	23	13
SY036	1	G2a	SV088	15	15	17	11	29	22	11	10	14	16	10	12	21	15	16	21	11
SY037	1	I2	SV090	16	12	14	13	30	23	10	11	13	15	11	13	20	15	19	21	11
SY038	1	G2a	SV093	16	15	16	12	28	22	10	10	14	14	10	12	21	14	16	21	13
SY039	1	G2a	SV094	16	11	14	12	28	20	10	11	14	16	10	12	21	15	17	21	11
SY040	2	G2a	SV096, SV150	16	15	16	12	28	22	10	10	14	14	10	13	21	15	16	21	13
SY041	1	R1a	SV099	16	11	14	13	30	25	11	11	13	14	11	10	19	17	15	23	13
SY042	1	G2a	SV101	15	15	16	12	30	22	10	10	14	16	10	12	21	16	17	21	11
SY043	1	G2a	SV102	15	13	14	12	29	22	10	11	14	16	10	11	20	16	18	21	12

SY044	1	G2a	SV103	15	15	17	12	29	22	10	10	14	16	10	13	21	15	22	11
SY045	1	G2a	SV104	15	15	16	12	30	22	10	10	14	16	10	12	21	15	17	11
SY046	3	G2a	SV114, SV167, SV169	15	15	17	12	28	22	10	10	14	16	10	12	21	16	16	11
SY047	1	J2a1	SV122	15	15	15	13	29	22	11	11	12	14	9	14	21	16	15	12
SY048	2	G2a	SV128, SV130	15	15	18	12	28	22	10	10	14	16	8	11	21	15	17	11
SY049	1	G2a	SV132	15	15	15	12	29	22	11	10	14	16	10	12	21	16	17	11
SY050	1	R1a	SV133	16	11	14	13	30	24	11	11	13	14	11	10	19	16	15	13
SY051	1	G2a	SV134	15	15	18	11	28	22	11	10	14	16	10	12	21	15	17	11
SY052	3	G2a	SV136, SV142, SV144	15	15	16	12	29	22	10	10	14	16	10	11	19	16	17	11
SY053	1	R1a	SV137	16	11	15	13	30	25	11	11	13	14	11	10	19	18	15	13
SY054	1	R1a	SV140	16	11	14	13	30	25	10	11	13	14	11	10	19	16	16	13
SY055	1	G2a	SV141	15	15	17	11	28	22	11	10	14	16	10	13	21	15	18	11
SY056	1	G2a	SV143	15	17	17	12	29	22	10	10	14	16	10	11	21	15	16	11
SY057	1	J2a1	SV145	14	14	16	14	31	26	10	11	12	16	9	12	20	15	18	11
SY058	1	G2a	SV147	15	15	17	12	29	22	10	10	14	16	10	11	21	15	16	11
SY059	1	G2a	SV152	15	15	16	12	28	22	10	10	14	16	10	11	21	16	18	11
SY060	1	G2a	SV153	15	15	17	12	29	22	10	10	14	16	10	11	21	16	17	12
SY061	1	J2a1	SV154	15	14	16	13	29	25	10	11	12	16	9	13	20	15	17	12
SY062	1	G2a	SV155	15	15	17	11	29	22	11	10	14	16	10	12	21	15	16	11
SY063	1	G2a	SV158	15	15	17	12	30	22	10	10	14	16	8	11	21	15	18	11
SY064	1	G2a	SV159	15	15	17	12	29	22	10	11	14	16	10	11	21	16	17	12
SY065	1	G2a	SV161	15	15	15	12	29	22	10	10	13	16	10	11	21	15	17	11
SY066	1	G2a	SV163	15	16	16	12	29	22	11	10	14	16	10	11	21	16	16	11

SV067	2	G2a	SV165, SV166	15	15	17	12	29	22	10	10	10	14	15	8	11	21	15	18	21	11
SV068	1	G2a	SV170	15	15	16	12	29	22	10	10	10	14	16	10	11	21	16	16	19	11
SV069	1	G2a	SV179	15	15	16	12	29	22	10	10	10	14	16	10	11	21	15	17	21	11
SV070	1	G2	SV180	15	15	17	12	28	22	10	10	10	14	16	10	12	20	16	16	21	11
SV071	1	G2a	SV183	15	15	16	12	28	22	10	10	10	14	16	10	12	21	16	16	21	11
SV072	1	G2a	SV187	15	15	16	12	28	22	10	10	10	14	16	10	11	21	16	19	21	11

Appendix 9. Haplogroup frequencies for Svans and comparative populations

Pop	Ab	Ad	Ar	Av	Ch	Ci	CT	Dr	Ge	Ir	Ka	Kr	Le	MJ	KN	Om	ON	OS	Pa	Qa	Sa	Sv	Sy	UAE	Uz	Ye
<i>n</i>	136	155	36	61	176	123	20	45	76	116	150	106	46	23	130	105	138	24	118	90	553	184	119	131	20	221
A	1	0	0	0	0	1	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0
B	0	1	0	3	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	1	0
C	8	2	0	0	2	7	0	0	0	0	10	0	0	0	18	0	2	0	0	0	0	7	0	0	1	0
D	4	1	0	0	2	5	0	0	2	0	5	1	2	0	13	0	11	1	0	0	0	3	0	0	4	0
F	1	0	0	0	0	0	0	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0	1	0
G	0	0	0	0	0	1	0	0	0	0	0	5	0	0	7	0	1	0	0	0	0	0	0	0	1	0
H	32	57	12	14	43	23	0	6	11	41	21	27	11	1	26	14	25	2	30	12	51	35	35	24	0	16
HV	4	6	4	5	2	5	4	4	1	0	7	1	0	0	3	2	12	2	1	1	4	0	3	0	3	2
I	3	5	1	1	8	0	1	1	6	0	2	4	2	1	2	1	0	1	0	3	5	3	3	0	0	1
J	2	2	2	1	6	13	2	3	4	15	12	6	6	13	0	16	17	1	12	16	117	1	10	14	1	25
K	5	13	1	8	10	9	2	7	3	6	9	4	5	0	0	9	12	4	10	3	23	29	7	13	0	15
L	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	19	0	0	20	14	57	0	8	12	0	84
M	1	1	0	0	2	5	0	1	0	1	2	1	0	0	3	5	4	1	2	9	38	2	0	10	1	19
N*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	1	14	0	1
N1	0	1	1	0	6	0	1	2	1	2	1	0	0	0	0	3	2	0	3	1	40	2	2	4	0	11
N2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N9	0	0	0	0	4	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
R	8	8	2	0	3	4	0	2	3	5	3	3	4	0	0	0	1	0	3	7	99	1	5	8	4	13

T	6	14	6	1	34	12	6	2	10	11	15	10	2	5	4	18	8	3	18	2	36	17	18	5	1	5
U*	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	2	0	1	2	1	6	3	3	2	0	4
U1	9	2	1	5	2	4	1	3	3	2	5	17	0	0	3	0	7	0	1	1	5	14	6	2	1	4
U2	5	4	0	0	6	6	0	0	3	2	7	6	0	0	7	0	3	2	1	2	4	11	1	3	0	5
U3	10	7	4	0	8	8	2	0	1	7	15	10	3	0	3	5	6	0	1	0	15	4	8	2	0	2
U4	7	3	0	4	8	1	1	0	10	0	3	2	3	0	2	0	1	1	0	0	0	4	0	0	0	0
U5	10	15	0	8	15	3	0	0	3	2	11	6	6	1	2	0	10	1	1	1	3	5	2	2	0	2
U6	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	5	4	3	0	0	2
U7	0	1	0	0	3	0	0	2	1	3	0	0	0	0	1	2	0	2	3	4	4	3	3	1	0	2
U8	0	0	0	0	0	6	0	0	1	1	1	0	0	2	3	6	0	0	1	8	3	0	0	8	0	2
U9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	2
V	0	0	0	3	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
W	7	7	0	5	7	4	0	0	3	0	9	1	0	0	2	0	4	1	2	2	7	23	0	5	0	0
X	13	5	1	3	3	2	0	12	10	2	10	2	2	0	8	0	9	1	6	1	15	13	1	2	0	4
Y	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Z	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	1	0
TOT	136	155	36	61	176	123	20	45	76	116	150	106	46	23	130	105	138	24	118	89	553	184	119	131	20	221

KEY: Ab=Abkhaz; Ad=Adygei; Ar=Armenian; Av=Avar; Ch=Chechen; Ci=Circassian; CT=Crimean Tatar; Dr=Druze; Ge=Georgian; Ir=Iraqi; Ka=Kabardine; Kr=Karachay; Lez=Lez; MJ=Mountain Jew; KN=Kara Nogai; Om=Omani; ON=North Ossetian; OS=South Ossetian; Pa=Palestinian; Qa=Qatari; Sa=Saudi; Sv=Svan; Sy=Syrian; UAE=Emereti; Uz=Uzbek; Ye=Yemeni.

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