© Kamla-Raj 2019 Int J Hum Genet, 19(1): 29-47 (2019)
PRINT: ISSN 0972-3757 ONLINE: ISSN 2456-6330 DOI: 10.31901/24566330.2019/19.01.709

Matrilineal and Patrilineal Genetic Continuity of Two Iron Age Individuals from a Pazyryk Culture Burial

Dmitrii G. Tikhonov[1], Cemal Gurkan[2, 3,*], Gokce Y. A. Peler[4] and Victor M. Dyakonov[5]

[1]Scientific Research Institute of Health, North-Eastern Federal University, Yakutsk, Sakha Republic, Russian Federation
[2]Turkish Cypriot DNA Laboratory, Committee on Missing Persons in Cyprus Turkish Cypriot Member Office, Nicosia (North Cyprus), Turkey
[3]Dr. Fazil Kucuk Faculty of Medicine, Eastern Mediterranean University, Famagusta, (North Cyprus), Turkey
[4]Department of Contemporary Turkic Languages and Literatures, Erciyes University, Kayseri, Turkey
[5]Archaeology Department, Institute for Humanitarian Research and Problems of Indigenous People of the North, Siberian Branch of the Russian Academy of Sciences, Yakutsk, Sakha Republic, Russian Federation

KEYWORDS Ak-Alakha. Ancient DNA. Scythian. Saka. Turkic

ABSTRACT In this study, geographic and linguistic distributions of contemporary and ancient matches with the paternal and maternal lineages of two individuals exhumed from the exemplary Pazyryk culture burial site of Ak-Alakha-1 mound 1 were investigated. Using the shared paternal and maternal haplotypes observed in both ancient individuals, extensive database and literature searches were conducted revealing numerous full matches among contemporary Eurasians, majority of whom speak Altaic Languages. Despite the current focus on the two Pazyryk individuals, a rare glimpse into the ancient migrations was gained through the discovery of paternal and maternal haplotype matches across an immense geography that spans from Yakutia to Turkey. In addition to a vast array of archaeological findings in such Scythian "frozen graves" across Central Asia, accumulating archaeogenetic data are expected to shed light on the anthropology of these otherwise mysterious people.

INTRODUCTION

Scythians were nomadic pastoralists who lived between the 9th and 1st centuries BCE. They inhabited a vast geography spanning the Eurasian Steppe, starting from the Vistula River in Eastern Europe, through the Central Asia, and finally reaching the Tarim Basin in Northwest China. Such a spatial and temporal expanse naturally entailed contacts with numerous other civilizations of the time, which is reflected by the different names attributed to the Scythians in ancient records such as the *Skyth(ai)* by the Greeks, *Saka* by the Persians, *Sai* by the Chinese, *Asgus(ai)* by the Assyrians, and *Ishkigulu* by the Urartians (King and Thompson 1907; Herodotus 1920; Luckenbill 1927; Ercilasun 2008; Durmus 2012).

From the linguistic perspective alone, the ethnonyms associated with the Scythians may perhaps have an Old Turkic and/or Mongolic root to start with. Briefly, the ancient Persian terminology of *Saka* is reminiscent of the Turkic word *yaqa* for 'coast, shore or edge', of course, being an Iranized version of the word with a *y*- to *s*- sound change. Intriguingly, the contemporary Turkic population of Yakuts also call themselves *Sakha*, which is seemingly the Yakut equivalent of the general Turkic word *yaqa* [*y- to s- sound change is typical of the Yakut language, and one of the characteristics that differentiate it from the other Turkic languages*] (Kirliscioglu 1994; Stachowski and Menz 2006). The ancient Greek terminology, which has found the most widespread use today, parallels the ancient Persian one. According to Herodotus, the *Skythai* and *Saka* were the same people (Herodotus 1920). Curiously, when the Greek plurality marker *–ai* is removed, the remaining part, *Skyt(h)*, seems to retain the Old Turkic and Mongolic plurality marker *–t*. Hence, the Greek version could be a Grecified version of the originally Turkic-Mongolic *Saqat* or *Saqït* (Ercilasun 2008). Incidentally, the Scythian tribe names

---

[*]*Address for correspondence:*
E-mail: cemal.gurkan@gmail.com

Targutae, *Skolot* and *Paralat* also end with the sound *–t* and hence could be interpreted as *Türküt*, *Sikülüt* and *Barulat*, in turn being the plural forms of the Turkic tribal names *Türk, Çiğil* and *Barula* (Zeki Velidi Togan 1981).

The debate around the population continuity associated with the ancient Scythians is still an unsettled one. Minns could not have been more correct in stating more than a century ago that *"Perhaps no question touching the ethnography of the ancient world has been more disputed than that of the affinities of the Scythians"* (Minns 1913; Kristiansen 1998; Damgaard et al. 2018). Indeed, more than a few different ethnic affinities were proposed for the Scythians, such as Iranian, Uralic-Altaic (proto-Turkic) and Slavonic being the most prominent and persistent ones (Denis 1990; Mallory and Adams 1997; Findley 2004; Beckwith 2009; Cynarski 2018). The most convincing proposal for the ethnic origins of the ancient Scythians remains the possibility that *"They were not a specific people"*, but rather one that comprised a variety of ethnicities *"referred to at variety of times in history, and in several places, none of which was their original homeland"* (Kristiansen 1998).

The Scythian cultural heritage is evident from the legacy of an immense array of artifacts left behind, such as those recovered at numerous kurgan burials across the Eurasian Steppe. At least in the archaeological context, the terms Scythian and Scythic are used interchangeably without a specific linguistic or ethnic connotation to imply a broader display of mounted nomadic characteristics associated with the Scytho-Siberian culture, such as the presence of special weapons, horse gear and of course "the animal style" artwork (Davis-Kimball 1995; Di Cosimo 1999). Among these, the most notable is "the animal style", the development of which was seemingly influenced by two important progressive steps in human civilization: the emergence of metal processing and progress in animal husbandry. In the Scythian period, "the animal style" had become an integral art form used for decorating everyday objects such as horse gears, jewelry, weapons, mirrors, handled wine jugs, cups, vases, batons, calyptras, appliqués, shields, plaques, saddlery, belts etc. Furthermore, it was also apparently used as symbols on banners (Roux 1997).

While it was originally thought that the Pontic-Caspian Steppe, situated just above the Black Sea, was the heartland for the Scythian culture, a more recent hypothesis suggested Central Asia as a more likely origin (Bashilov and Yablonsky 2000; Yablonsky 2000). The strongest support for a Central Asiatic origin stems from the discovery of the earliest Scythian kurgan in Tuva from Southern Siberia (Grjaznov 1984). Potential Asiatic origins for "the animal style" artistic traditions also provide further support for the Central/East Asian origin of this culture (Bashilov and Yablonsky 2000). Fortunately, special environmental circumstances associated with the Siberian permafrost provided a unique opportunity for the recovery of highly preserved Scythian human remains and associated organic artifacts, as part of "frozen grave" burials that are dated between 6th and 3rd centuries BCE. Scythian burials, such as those associated with the Pazyryk culture, were found at numerous sites across the Altai Mountains, modern-day Kazakhstan and Mongolia. Along with these unique archaeological findings, an increasing amount of anthropological and archaeogenetic data collectively suggest an admixed genetic and cultural character for the Scythians comprising west and east Eurasian influences (Alekseev 1986; Voevoda et al. 1998; Voevoda et al. 2000; Clisson et al. 2002; Chikisheva 2003; Lalueza-Fox et al. 2004; Ricaut et al. 2004a; Ricaut et al. 2004b; Pilipenko et al. 2010; Pilipenko et al. 2015; Gubina et al. 2016; Juras et al. 2017; Movsesian and Bakholdina 2017; Damgaard et al. 2018).

Of particular interest to the current study are the archaeogenetic investigations associated with the exemplary mound 1 from the Ak-Alakha-1 site on the Ukok Plateau in the Altai Republic (Polosmak 1994a; Pilipenko et al. 2015). This typical Pazyryk "frozen grave" was dated around 2268±39 years before present (Bln-4977) (Gersdorff and Parzinger 2000). Initial anthropological findings suggested an undisturbed dual inhumation comprising "a middle-aged European-type man" and "a young European-type woman", both of whom presumably had a high social status among the Pazyryk elite (Polosmak 1994a). In contrast, recent archaeogenetic investigations revealed somewhat contradicting results since analyses at both the amelogenin gene and Y-chromosome short tandem repeat (Y-STR) loci clearly established that both Scythians were actually males and had paternal and maternal lineages that are typically associated with eastern Eurasians (Pilipenko et al. 2015). Through the use of mitochondrial, autosomal and Y-chromosomal DNA typing systems, it was possible to not only investigate the potential relationships between the two ancient Scythians but also to gather initial phylogenetic and phylogeographic information on their paternal and maternal lineages (Pilipenko et al. 2015). Archaeogenetic data also helped to establish that the two ancient Scythians had (a) the same mitochondrial hypervariable region 1 (HVR1) profile, hence both had a shared/closely related maternal lineage, (b) possibly the same or a closely related paternal lineage, since the two individuals had a full match across 12 loci at which data was available for both individuals, but (c) the absence of a first-degree kinship due to the exclusions at three out of six autosomal STR loci. The shared mitochondrial HVR1 profile, which was subsequently confirmed elsewhere, corresponded to the east Eurasian haplogroup C (C4a1+16129), which is observed frequently in the gene pool of the Pazyryk people from other burial sites, such as at Ak-Alakha-5, Ala-Gail-2 and Berel', as well as that of contemporary Altaians (Derenko et al. 2003; Derenko et al. 2007; Gubina et al. 2013; Pilipenko et al. 2015; Unterlander et al. 2017). Based on the Y-STR data available, the two Ak-Alakha-1 Scythians had an *in silico* haplogroup assignment of N, which first appeared in southeastern Asia and then expanded in southern Siberia (Rootsi et al. 2007; Pilipenko et al. 2015).

Objectives

Current study aims to investigate the geographical distributions of the ancient and contemporary matches and close genetic variants of the maternal and paternal lineages observed in the two Scythians from the exemplary Ak-Alakha-1 kurgan. An effort is also made to present the contemporary matches of both types of haplotypes in a linguistic context.

METHODOLOGY

Potential matrilineal and patrilineal genetic continuity of the Pazyryk culture population was investigated based on already available archaeogenetic data for two individuals exhumed from the Ak-Alakha-1 Pazyryk burial site (Pilipenko et al. 2015). Y-STR haplotypes matching with or having only a few allelic variations from that observed in the two Scythians from Ak-Alakha-1 were compiled through searches at the Y-Chromosome STR Haplotype Reference Database (YHRD), Y-Search Utility of the Laboratory of Human Population Genetics, Research Centre of Medical Genetics, Moscow, and literature (Willuweit and Roewer 2015; Chukhryaeva et al. 2016). In cases where the Y-chromosomal SNP based haplogroup assignments were not available, the online 21-haplogroup version of the Whit Athey haplogroup assignment algorithm was used instead (Athey 2006). Median-joining network (M-JN) analysis was carried out with a 17-loci (DYS456, DYS389I, DYS390, DYS389II, DYS458, DYS19, DYS385a/b, DYS393, DYS391, DYS439, DYS635, DYS392, Y-GATA-H4, DYS437, DYS438, and DYS448) Y-STR dataset that was compiled from the literature and using the Network v.5.0.0.0 software as previously described (Bandelt et al. 1999; Gurkan et al. 2017). mtDNA (HVR1, 16024-16365) haplotypes matching with those observed in the two ancient Scythians were compiled through searches at the EMPOP database and literature (Parson and Dur 2007). Close variants of the PZ1 mtDNA HVR1 haplotype with a single missing or additional mutation were also compiled, albeit only from relevant archaeogenetic studies.

RESULTS

Searches for full 17-loci matches with the Ak-Alakha-1 Y-STR haplotype (PZ1) revealed 15 such haplotypes among the contemporary populations across the Eurasian geography that belonged to: (a) 10 Turkic-speaking individuals from Turkey, Afghanistan and Russia (five Turkish, three Turkmen, one Tatar and one Uzbek), (b) three individuals from the Muslim Hui and Dongxiang minorities in China, (c) one Tajik individual from Afghanistan, and (d) one individual of an unspecified ethnic background from Russia (Table 1a). Notably, the only match between the PZ1 Y-STR haplotype and another ancient DNA sample was that from a 15th century CE Yakut individual, although at only 12 loci

Table 1a: Matches with and/or close variants of the ancient Ak-Alakha-1 (PZ1) 17-loci Y-STR haplotype†

ID	*DYS456*	*DYS389I*	*DYS390*	*DYS389II*	*DYS458*	*DYS19*	*DYS385a/b*	*DYS393*	*DYS391*	*DYS439*	*DYS635*	*DYS392*	*Y-GATA-H4*	*DYS437*	*DYS438*	*DYS448*	*Hg*	*Population ID‡*
PZ1[1]	15	13	23	29	16	14	12, 13	13	10	10	24	14	12	14	10	18	N[2]	PZ1 (1) (Pilipenko et al. 2015)
1	*15*	*13*	*23*	*29*	*16*	*14*	*12, 13*	*13*	*10*	*10*	*24*	*14*	*12*	*14*	*10*	*18*	N[2]	DON (1) [YA003978/YA004178 (*GAN*)] HUI (2) [YA004121 (*XIN*); YA003841/ YA004065/YA004182 (*GAN*)] TUR [YA004119 (*MAR*) (2), YA003668 (*CUK*) (1), YA004115 (*BS*) (2)]
2	15	13	23	29	16	14	12, 13	13	10	10	24	**13**	12	14	10	18	N[2]	TUR (2) [YA004115 (*BS*)]
3	15	13	23	29	16	14	12, 13	13	10	10	**23**	14	12	14	10	18	N[2]	TUR (2) [YA004119 (*MAR*)]
4	15	13	23	29	16	14	12, 13	13	10	10	24	14	12	14	**11**	**19**	N[2]	TUR (1) [YA004171 (*BandH*)]
5	15	13	23	29	16	14	12, 13	13	10	**11**	24	14	12	14	10	18	N[2]	TUR (1) [YA003719/YA003907]
6	15	13	23	29	16	14	12, 13	13	10	**11**	**25**	14	12	14	10	18	N[2]	TUR (1) [YA003719/YA003907]
7	15	13	23	29	16	**13**	12, 13	13	10	10	24	14	12	14	10	18	N[2]	TUR (1) [YA003719/YA003907]
8	15	13	23	**30**	16	14	12, 13	13	10	10	24	14	12	14	10	18	N[2]	DON (2) [YA003978/YA004178 (*GAN*)] HUI (1) [YA004176 (*QIN*)] TUR (1) [YA004116 (*CA*)]
9	15	13	23	29	16	14	12, 13	13	10	10	**25**	14	12	14	10	18	N[2]	DON (2) [YA003978/YA004178 (*GAN*)]
10	15	13	23	29	**15**	14	12, 13	13	10	10	24	14	12	14	10	**19**	N[2]	MAN (1) [YA004169]
11	15	13	23	29	16	14	12, 13	13	10	10	**23**	14	12	14	10	**19**	N[2]	MAN(1) [YA004169] KHL (1) [YA003670] MON (1) [YA003298/ YA003909/YA004067/YA004136 (*IMC*)]
12	15	13	23	29	**15**	14	12, 13	13	10	**11**	**23**	14	12	14	10	**19**	N[2]	HAN (1) [YA003440/YA004082]
13	15	13	23	29	16	14	12, 13	13	10	10	**22**	14	**11**	14	10	18	N[2]	HUI (1) [YA004065/YA004182 (*GAN*)]
14	15	13	23	29	**17**	14	12, 13	13	10	10	24	14	**11**	14	10	**19**	N[2]	KAZ (1) [YA003979]
15	15	13	23	29	16	14	12, 13	13	10	10	24	14	12	14	10	**19**	N[2]	KHL (1) [YA003737 (*CMO*)] MON (2) [YA004127 (*ULA*)]
16	15	13	23	29	16	14	12, 13	13	10	10	24	14	**11**	14	10	18	N[2]	KHL (1) [YA003737 (*CMO*)]
17	15	13	23	29	**17**	14	12, 13	13	10	10	24	14	**11**	14	10	18	N[2]	UIG (1) [YA003847/YA004122]
18	15	13	23	29	**17**	14	12, 13	13	10	**11**	24	14	12	14	10	18	N[2]	KHL/BUR/DAR (1) [YA003736] KHL/ UUL/BUR (1) [YA003735]
19	15	13	23	**28**	16	14	12, 13	13	10	10	24	14	12	14	10	**20**	N[2]	KHL (1) [YA003670]
20	15	13	23	**28**	16	14	12, 13	13	10	10	24	14	12	14	10	**19**	N[2]	MCH (1) [YA003981] MON (2) [YA004127 (*ULA*)]
21	15	13	23	29	16	14	12, 13	13	10	10	24	14	**11**	14	10	**19**	N[2]	MON (1) [YA004127 (*ULA*)]
22	15	13	23	**28**	16	14	12, **14**	13	10	10	24	14	12	14	10	**19**	N[2]	NHA (1) [YA003756]
23	**16**	13	23	29	16	14	12, 13	13	10	10	24	14	**11**	14	10	18	N[2]	RUS (1) [YA004184]
24	15	13	23	29	**17**	14	12, 13	13	10	10	24	14	12	14	10	**19**	N[2]	RUS (3) [YA003678 (*SVE*)/ YA004184]

Table 1a: Contd....

ID	*DYS456*	*DYS389I*	*DYS390*	*DYS389II*	*DYS458*	*DYS19*	*DYS385a/b*	*DYS393*	*DYS391*	*DYS439*	*DYS635*	*DYS392*	*Y-GATA-H4*	*DYS437*	*DYS438*	*DYS448*	*Hg*	*Population ID*[‡]
25	15	13	23	**28**	16	14	12, **14**	13	10	10	24	14	12	14	10	18	N[2]	UIG (1) [YA003847/YA004122]
26	15	13	23	29	**17**	14	12, 13	13	10	**11**	24	14	12	14	10	**19**	N[2]	YAK (1) [YA004128]
27	15	13	23	**30**	16	14	**13**, 13	13	10	10	24	14	12	14	10	**19**	N1b	YAK (1) (Karmin et al. 2015)
28	**13**	13	23	29	**17**	14	12, 13	13	10	10	24	14	12	14	10	**19**	N[2]	CHU (1) [YA003960]
29	15	13	23	**31**	16	14	12, 13	13	10	10	24	14	12	14	10	18	N1c1	TAT (1) (Chukhryaeva et al. 2016)
30	*15*	*13*	*23*	*29*	*16*	*14*	*12, 13*	*13*	*10*	*10*	*24*	*14*	*12*	*14*	*10*	*18*	N(xN 1c1)	TAT (1) (Chukhryaeva et al. 2016)
31	15	13	23	29	16	14	12, 13	13	10	10	**25**	14	12	14	10	18	N(xN 1c1)	TAT (1) (Chukhryaeva et al. 2016)
32	15	13	23	**30**	**17**	14	12, 13	13	10	10	24	14	**11**	14	10	18	N1b	UKR (1) (Chukhryaeva et al. 2016)
33	**16**	13	**24**	29	16	14	12, 13	13	10	10	24	14	12	14	10	18	N1	NOG (2) (Chukhryaeva et al. 2016)
34	15	13	23	29	16	14	12, **14**	13	10	10	**26**	14	12	14	10	18	N(xN 1c1)	TAT (1) (Chukhryaeva et al. 2016)
35	**16**	13	23	**30**	16	**13**	12, 13	13	10	10	24	14	12	14	10	18	N1b	RUS (1) (Chukhryaeva et al. 2016)
36	15	13	23	29	16	14	12, 13	13	**11**	10	24	14	12	14	10	**19**	N1b	KHA (1) (Mirabal et al. 2009)
37	15	13	23	29	16	14	12, 13	13	10	10	24	14	12	14	10	**19**	N1b	KHA (9) (Mirabal et al. 2009)
38	15	13	23	**30**	16	14	12, 13	13	10	10	24	14	12	14	10	**19**	N1b	KHA (1) (Mirabal et al. 2009)
39	15	13	23	29	16	14	12, 13	13	10	**11**	24	14	12	14	10	**19**	N1b	KHA (1) (Mirabal et al. 2009)
40	15	13	23	**30**	16	14	12, 13	13	10	10	**23**	14	12	14	10	**19**	N1b	KHA (1) (Mirabal et al. 2009)
41	*15*	*13*	*23*	*29*	*16*	*14*	*12, 13*	*13*	*10*	*10*	*24*	*14*	*12*	*14*	*10*	*18*	N-P43	TAJ (1), TMN (3) and UZB (1) (Di Cristofaro et al. 2013)
42	15	13	**24**	29	16	14	12, 13	13	10	10	24	14	**13**	14	10	18	N-P43	UZB (1) (Di Cristofaro et al. 2013)
43	15	13	23	**30**	**17**	14	12, 13	13	10	10	**23**	14	12	14	10	18	N-P43	TMN (1) (Di Cristofaro et al. 2013)
44	15	13	23	**30**	16	14	12, 13	13	10	10	24	14	12	14	10	18	N-P43	TAJ (1) (Di Cristofaro et al. 2013)
45	15	13	23	**28**	16	14	12, 13	13	10	10	**23**	14	12	14	10	**19**	N-P43	MON (1) (Di Cristofaro et al. 2013)
46	15	13	23	29	16	14	12, 13	13	10	10	24	14	12	14	10	**19**	N-P43	MON (1) (Di Cristofaro et al. 2013)
47	15	13	23	29	16	14	12, 13	13	10	10	**23**	14	12	14	10	**19**	N-P43	MON (1) (Di Cristofaro et al. 2013)
48	15	13	**24**	**30**	16	14	12, 13	13	10	10	**25**	14	12	14	10	18	N-P43	MON (1) (Di Cristofaro et al. 2013)
49	15	**14**	23	29	16	14	12, 13	13	10	10	24	14	12	14	10	18	N-P43	MON (1) (Di Cristofaro et al. 2013)
50	15	13	23	29	**17**	14	12, 13	13	10	10	24	14	12	14	10	**19**	N1b[*]	CHL (1) (Dulik et al. 2012)
51	15	13	23	29	**17**	**15**	12, 13	13	10	10	24	14	12	14	10	**19**	N1b[*]	CHL (2) (Dulik et al. 2012)
52	15	13	23	29	**17**	14	12, 13	13	10	10	24	14	**13**	14	10	**19**	N1b[*]	CHL (1) (Dulik et al. 2012)
53	*15*	*13*	*23*	*29*	*16*	*14*	*12, 13*	*13*	*10*	*10*	*24*	*14*	*12*	*14*	*10*	*18*	N2	RUS (1) (Balanovsky et al. 2008)
54	15	13	**24**	29	16	14	12, **14**	13	10	10	24	14	12	14	10	18	N2	RUS (1) (Balanovsky et al. 2008)
55[1]	-	13	23	29	-	14	12, 13	13	10	10	-	14	-	14	10	-	K(xN, O,P)	aYK (1) (Crubezy et al. 2010)
56	-	13	23	29	-	14	-	13	10	10	-	14	-	-	-	-	N1b	KKP (2) (Balaresque et al. 2015)

Table 1a: Contd....

ID	*DYS456*	*DYS389I*	*DYS390*	*DYS389II*	*DYS458*	*DYS19*	*DYS385a/b*	*DYS393*	*DYS391*	*DYS439*	*DYS635*	*DYS392*	*Y-GATA-H4*	*DYS437*	*DYS438*	*DYS448*	*Hg*	*Population ID*‡
57	-	**14**	23	29	-	14	-	13	10	10	-	14	-	-	-	-	N1c1	KKP (2) (Balaresque et al. 2015)
58	-	13	23	29	-	14	-	**14**	10	10	-	14	-	-	-	-	N1c1	KKP (1) (Balaresque et al. 2015)
59	-	13	23	29	-	14	-	13	10	**11**	-	14	-	-	-	-	N1b	TMN (1) (Balaresque et al. 2015)
60	-	13	23	**30**	-	14	-	**12**	10	**11**	-	14	-	-	-	-	N1b	TMN (1) (Balaresque et al. 2015)
61	-	13	23	29	-	14	-	13	10	10	-	**15**	-	-	-	-	N1b	UZB (1) (Balaresque et al. 2015)
62	-	13	23	29	-	**13**	-	13	10	10	-	14	-	-	-	-	N1b	TAJ (2)] (Balaresque et al. 2015)
63	-	13	23	29	-	14	12,13	13	10	10	-	14	-	14	10	-	N2-A	KHA (5), MAN (9) (Pimenoff et al. 2008)
64	-	13	23	29	-	14	**13**,13	13	10	10	-	14	-	14	10	-	N2-A	KHA (1) (Pimenoff et al. 2008)
65	-	13	23	29	-	14	-	13	10	10	-	14	-	14	10	-	N*-M231	TUR (4) (Cinnioglu et al. 2004)
66	-	13	23	29	-	14	-	13	10	10	-	14	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
67	-	13	23	29	-	14	-	13	10	**11**	-	14	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
68	-	13	23	29	-	14	-	13	10	10	-	**13**	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
69	-	**11**	23	**27**	-	14	-	13	10	10	-	14	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
70	-	13	23	**28**	-	14	-	13	10	10	-	14	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
71	-	**14**	23	**30**	-	14	-	**14**	10	10	-	**13**	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
72	-	13	23	29	-	**15**	-	13	**11**	10	-	14	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
73	-	13	23	29	-	**15**	-	13	10	10	-	14	-	14	10	-	N*-M231	TUR (1) (Cinnioglu et al. 2004)
74	-	13	23	**30**	-	14	-	13	10	10	-	14	-	14	10	-	N*-M231	TUR (2) (Cinnioglu et al. 2004)

†17-loci Y-STR haplotypes matching with the original Scythian haplotype (PZ1) are shown in italics, while those with only a few allelic variations are shown in bold fonts at the differing loci. The only exceptions are haplotypes 55-74 that were typed with different Y-STR systems and have only partial loci overlap with the PZ1 haplotype. Further matches among non-PZ1 haplotypes are: 8 with 44, 9 with 31, 10 with 47, 15 with 37 and 46, 24 with 50. ‡Abbreviations for the population ID's (number of samples) (YHRD accession number or reference): PZ1, Ak-Alakha-1 (Pazyryk culture, 4th-3rd centuries BCE) – Ukok Plateau, Altai Republic; aYK (*BKH*: Balyktakh site, 15th century CE), Khangallassky, Yakutia Republic; DON, Dongxiang – Gansu, China; HUI, Hui – Xinjiang, China (*GAN: Gansu; QIN, Qinqai; XIN, Xinjiang*); TUR, Turkish – Turkey (*BS, Black Sea; CA: Central Anatolia; MAR: Marmara; CUK: Cukurova; BandH: Turkish expats in Bosnia and Herzegovina*); MAN, Eastern Mansi – Ural Republic; KHL, Khalkha – Mongolia (*CMO: Central Mongolia; ULA: Ulaanbaatar*); MON, Mongolian (*IMC: Inner Mongolia, China*); HAN, Han – Zhejiang, China; KAZ, Kazakh – Gansu, China; UIG, Uighur – Xinjiang, China; KHL/BUR/DAR, Khalkha, Buryat, Dariganga – Eastern Mongolia; KHL/UUL/BUR, Khalkha, Uuld, Buryat – Gobi, Mongolia; MCH, Manchu – Chengde, China; NHA, Northern Han – Liaoning, China; RUS, Russian – Russian Federation (*SVE: Sverdlovsk*); YAK, Yakut; CHU, Chuvash; TAT, Tatar; UKR, Ukrainian; NOG, Nogay; TAJ, Tajik; TMN, Turkmen; UZB, Uzbek; CHL, Chelkan; KKP, Karakalpak; KHA, Khanty. [1] Y-STR haplotypes from ancient DNA samples. [2] These haplogroup assignments were made with the Whit Athey Algorithm.

that was in common (Crubezy et al. 2010). There were also 75 additional near matches in contemporary populations from various Eurasian ethnicities, each having only a few allelic repeat differences from the 17-loci PZ1 Y-STR haplotype (Table 1a). Similar searches for full mtDNA HVR1 matches with the Ak-Alakha-1 mtDNA haplotype (PZ1) revealed 145 such haplotypes among contemporary Eurasian populations, plus 15 from among ancient cultures (Table 1b). While close variants of the PZ1 mtDNA haplotype among contemporary populations were too many to be listed in Table 1b, 18 close variants among ancient populations were included.

Figure 1 is a graphical illustration for the geographic distributions of the exact matches between the17-loci Y-STR and/or mtDNA HVR1 haplotype from Ak-Alakha-1 (PZ1) and those from contemporary and ancient populations. Among the noteworthy observations are: (a) matches between the PZ1 mtDNA haplotype and those from other ancient cultures are seemingly restricted to the Altai mountains and further to the east, although such conclusions could be somewhat biased considering the limitations on the amount of archaeogenetic data currently available, (b) matches between the PZ1 mtDNA haplotype and those from contemporary populations are more widespread and largely concentrated along a diagonal axis running from Yakutia in the northeastern Siberia, through the Central Asia and Caucasus, to Asia Minor; matches observed that are seemingly further away from this axis are still related with the ethnicities along the main axis (for example, Turkic, Mongolic, Tungusic and Uralic) (c) matches between the PZ1 17-loci Y-STR haplotype and those from contemporary populations have a narrower distribution and are mostly restricted to Turkic populations from Afghanistan, Russia and Turkey, although there are also three individuals from the Muslim minorities in China. Turkey is the only country wherein full matches with both the PZ1 17-loci Y-STR and mtDNA HVR1 haplotypes are observed, at least in the same ethnic group, that is, Turkish.

Table 2 provides a summary of the matches between the PZ1 Y-STR (17-loci) and mtDNA (HVR1) haplotypes and those of the contemporary and ancient populations, organized in terms of the language families that each sample is known to be associated with. The majority (66.7%) of the full 17-loci Y-STR matches among the contemporary populations are those from Turkic-speaking ethnicities, while the rest are distributed among ethnicities associated with Indo-European (13.3%), Mongolic (6.7%) and Sino-Tibetan language families (13.3%). The same trend continues for the close allelic variants of the PZ1 17-loci Y-STR haplotype observed among the contemporary populations with the following breakdown of language families associated with each ethnicity: Turkic (34.6%), Mongolic (28%), Tungusic (1.3%), Uralic (20%), Indo-European (10.7%) and Sino-Tibetan (5.3%). Notably, samples originating from ethnicities associated with the larger Altaic language family also account for 63.9 percent. A total of 145 full matches with the PZ1 mtDNA HVR1 haplotype were observed among the contemporary populations and with the following frequencies based on the language families of the associated ethnicities: Turkic (45.5%), Mongolic (15.2%), Tungusic (16.6%), Koreanic (0.7%), Uralic (9%), Indo-European (9.7%), Caucasian (1.4%), Sino-Tibetan (1.4%) and Afro-Asiatic (0.7%). Samples originating from ethnicities associated with the larger Altaic language family were found to comprise the excess majority with 77.9 percent. There were also 15 full matches between the PZ1 mtDNA haplotype and those originating from ancient cultures with the following breakdown: Pazyryk (20%), Tachtyk (6.7%), Xiongnu (13.3%), Jinggouzi (13.3%) and Yakut (46.7%). Finally, 18 close variants of the PZ1 mtDNA haplotype were also observed among the samples originating from ancient cultures with the following breakdown: Pazyryk (22.2%), Zevakino-Chilikta (5.6%), Xiongnu (22.2%), Jinggouzi (5.6%) and Yakut (44.4%).

Figure 2 depicts the M-JN for the matches and close allelic variants between the PZ1 17-loci Y-STR haplotype and those from contemporary populations. There is again a clear dominance throughout the entire network by the samples associated with the Altaic language family. There are four major star-like descent clusters around the haplotypic ancestral nodes of PZ1/1/30/41/53, 15/37/46, 8/44 and 24/50, wherein ethnicities associated with the Altaic languages are present in every case and often constitute the majority. Figure 3 depicts a phylogenet-

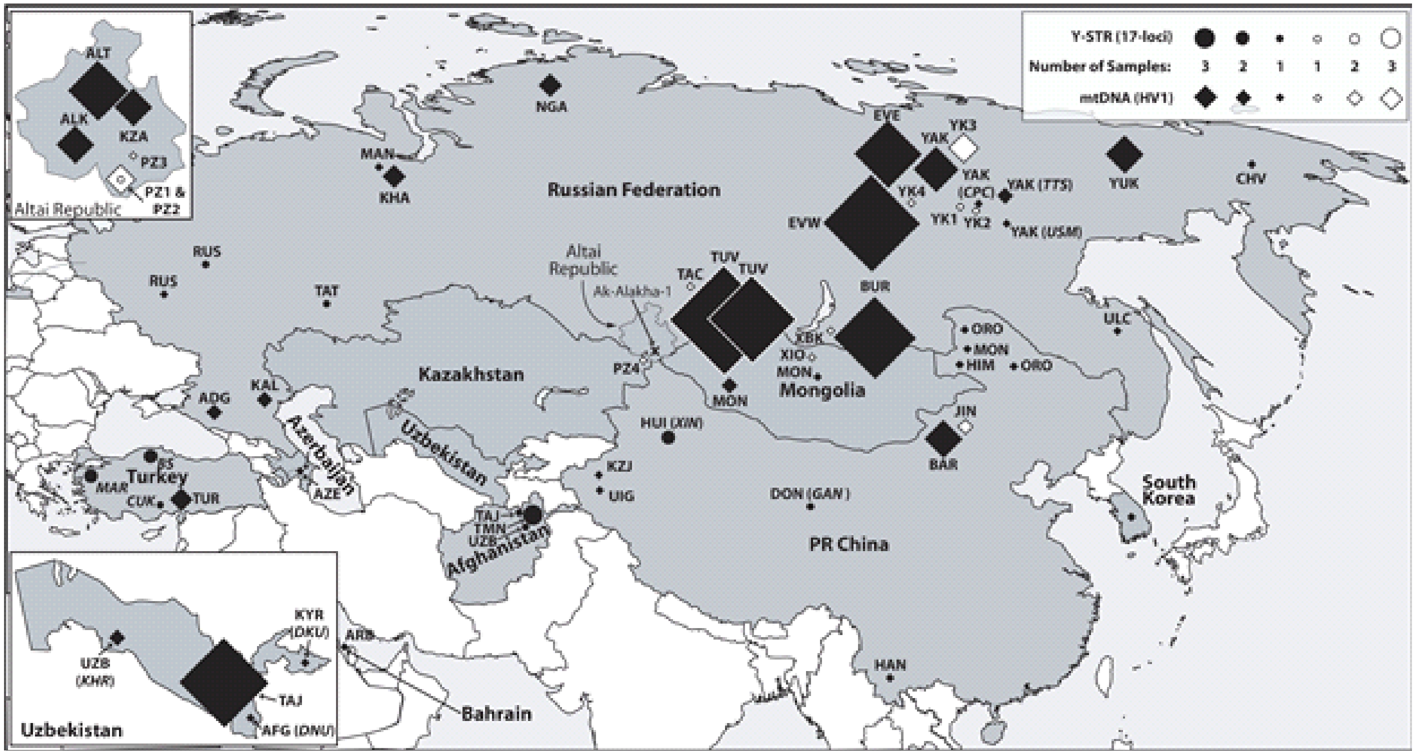

Fig. 1. Geographic distribution of the exact matches with the Scythian (PZ1) Y-STR (17-loci) and mtDNA (HVR1) haplotypes detailed in Tables 1a and 1b. Boundaries of the Altai Republic within the Russian Federation are shown with dashed lines, along with an approximate position of the Ak-Alakha-1 burial site, which is denoted with an 'x' on the map. Countries shaded in gray refer to those that have full 17-loci Y-STR and/or mtDNA HVR1 match(es) with the PZ1 haplotypes. Inset in the top and bottom left corners are the Altai and Uzbekistan maps, respectively, both scaled-up to allow better representation of the samples derived from these countries. There were no other exact matches from around parts of the globe that are not shown on the map, except for a single contemporary mtDNA haplotype from US, which presumably belonged to an 'East Asian' individual. Inset in the top right corner provides a scale for the number of haplotypes observed, but only up to three samples, which is valid for the entire map as well as the inset maps, irrespective of the differences in the scales of the actual map and inset maps themselves. For sample pools larger than three, the same linear scale provided on the inset in the top right corner still applies; please refer to Tables 1a and b for actual sample pool sizes. Samples are depicted on the entire map and the insets maps with circles and diamonds for the Y-STR and mtDNA haplotypes, respectively. Black and white coloring for samples depict whether the haplotype(s) are contemporary or ancient, respectively. Location of the PZ1 mtDNA and Y-STR haplotypes are shown on top of each other. Black diamonds representing the TUV samples have a white outline so as to help better visualize two separate sample pools from the same region.

Source: Author

Table 1b: Matches with and/or close variants of the ancient Ak-Alakha-1 (PZ1) mtDNA (HVR1) haplotype[†]

Haplotype ID	*mtDNA HVR1 profile*	*Hg*	*Population ID[‡]*
PZ1 [1]	16093C 16129A 16223T 16298C 16327T	C4a1 / C4a1+16129	PZ1 (2) (Pilipenko et al. 2015) (Unterlander et al. 2017)
1	*16093C 16129A 16223T 16298C 16327T*	C4a1	YAK (*TTS*) (2), (*USM*) (1), (*CPC*) (1) (Crubezy et al. 2010)
2	*16093C 16129A 16223T 16298C 16327T*	C4a1	UZB (*KHR*) (2) (Irwin et al. 2010)
3	*16093C 16129A 16223T 16298C 16327T*	C4a1	AFG (*DNU*) (1) (Irwin et al. 2010)
4	*16093C 16129A 16223T 16298C 16327T*	C4a1	KYR (*DKU*) (1) (Irwin et al. 2010)
5	*16093C 16129A 16223T 16298C 16327T*	C4a1	TAJ (12) (Irwin et al. 2010)
6	*16093C 16129A 16223T 16298C 16327T*	C4a1	RUS (1) (Malyarchuk et al. 2004)
7	*16093C 16129A 16223T 16298C 16327T*	C4a1	ARB (1) [AFDIL, 2012, *unpublished*]
8	*16093C 16129A 16223T 16298C 16327T*	C4a1	KOR (1) (Lee et al. 2006)
9	*16093C 16129A 16223T 16298C 16327T*	C4a1	EAU (1) [AFDIL, 2013, *unpublished*]
10	*16093C 16129A 16223T 16298C 16327T*	C	YAK (5) (Tarskaia and Melton 2006) and (1) (Derenko et al. 2007)
11	*16093C 16129A 16223T 16298C 16327T*	C4a1+16129+195	TUR (3) (Serin et al. 2016)
12	*16093C 16129A 16223T 16298C 16327T*	C4a1	BAR (5) (Derenko et al. 2012)
13	*16093C 16129A 16223T 16298C 16327T*	C	KZJ (1) (Yao et al. 2000)
14	*16093C 16129A 16223T 16298C 16327T*	C	UIG (1) (Yao et al. 2000)
15	*16093C 16129A 16223T 16298C 16327T*	C2b1	YUK (5) (Volodko et al. 2008)
16	*16093C 16129A 16223T 16298C 16327T*	C2b1	CHV (1) (Volodko et al. 2008)
17	*16093C 16129A 16223T 16298C 16327T*	C[*]	KHA (3) (Pimenoff et al. 2008)
18	*16093C 16129A 16223T 16298C 16327T*	C[*]	MAN (1) (Pimenoff et al. 2008)
19	*16093C 16129A 16223T 16298C 16327T*	C2b1	NGA (3) (Volodko et al. 2008)
20	*16093C 16129A 16223T 16298C 16327T*	C	AZE (1) (Richards et al. 2000)
21	*16093C 16129A 16223T 16298C 16327T*	C	ADG (2) (Macaulay et al. 1999)
22 [1]	*16093C 16129A 16223T 16298C 16327T*	C4	YK1 (1) and YK2 (1) (Crubezy et al. 2010)
23 [1]	*16093C 16129A 16223T 16298C 16327T*	C4	YK3 (4) and YK4 (1) (Keyser et al. 2015)
24 [1]	*16093C 16129A 16223T 16298C 16327T*	C4a1+16129	PZ2 (1) (Unterlander et al. 2017)
25 [1]	*16093C 16129A 16223T 16298C 16327T*	C4	PZ3 (1) (Unterlander et al. 2017)
26 [1]	*16093C 16129A 16223T 16298C 16327T*	C4a1+16129	PZ4 (1) (Unterlander et al. 2017)
27 [1]	*16093C 16129A 16223T 16298C 16327T*	C	TAC (1) (Keyser et al. 2009)
28 [1]	*16093C 16129A 16223T 16298C 16327T*	C	XIO (1) (Keyser-Tracqui et al. 2006)
29 [1]	*16093C 16129A 16223T 16298C 16327T*	C	JIN (2) (Wang et al. 2012)
30 [1]	*16093C 16129A 16223T 16298C 16327T*	C	XBK (1) (Pilipenko et al. 2018)
31	*16093C 16129A 16223T 16298C 16327T*	C	ALT (6) (Derenko et al. 2003), (2) (Gubina et al. 2013) and ALK (5) (Derenko et al. 2007)
32	*16093C 16129A 16223T 16298C 16327T*	C	BUR (2) (Derenko et al. 2003), (4) (Starikovskaya et al. 2005) and (5) (Derenko et al. 2007)
33	*16093C 16129A 16223T 16298C 16327T*	C	TUV (6) (Derenko et al. 2003), (9) (Starikovskaya et al. 2005) and (12) (Gubina et al. 2013)
34	*16093C 16129A 16223T 16298C 16327T*	C / C4	KZA (1) (Gokcumen et al. 2008) and KZA (4) (Derenko et al. 2012)
35	*16093C 16129A 16223T 16298C 16327T*	C	HAN (1) (Yao et al. 2002)
36	*16093C 16129A 16223T 16298C 16327T*	C	EVE (9) (Starikovskaya et al. 2005)
37	*16093C 16129A 16223T 16298C 16327T*	C	ULC (1) (Starikovskaya et al. 2005)

Table 1b: Contd...

Haplotype ID	*mtDNA HVR1 profile*	*Hg*	*Population ID*‡
38	*16093C 16129A 16223T 16298C 16327T*	C	MON (1) (Powell et al. 2007), (1) (Derenko et al. 2007) and (2) (Gokcumen et al. 2008)
39	*16093C 16129A 16223T 16298C 16327T*	C	ORO (1) (Powell et al. 2007) and (1) (Kong et al. 2003)
40	*16093C 16129A 16223T 16298C 16327T*	C	HIM (1) (Powell et al. 2007)
41	*16093C 16129A 16223T 16298C 16327T*	C	KAL (2) (Derenko et al. 2007)
42	*16093C 16129A 16223T 16298C 16327T*	C	EVW (13) (Derenko et al. 2007)
43 [1]	*16093C 16129A 16223T 16298C 16327T* **16362C**	C	BTG (1) (Gonzalez-Ruiz et al. 2012)
44 [1]	~~16093C~~ *16129A 16223T 16298C 16327T*	C	AA5 (1) (Unterlander et al. 2017), YK5 (1) (Crubezy et al. 2010), AA1 (1) and VK2 (1) (Gubina et al. 2016)
45 [1]	~~16093C~~ *16129A 16223T 16298C 16327T*	C	JIN (1) (Wang et al. 2012), XIO (1) (Keyser-Tracqui et al. 2006) and XBK (2) (Pilipenko et al. 2018)
46 [1]	*16093C* ~~16129A~~ *16223T 16298C 16327T*	C4(C4a1/C4b8/C4+152+16093)	ZEV (1) (Unterlander et al. 2017)
47 [1]	*16093C 16129A 16223T* ~~16298C~~ *16327T*	C4	YK6 (5) (Crubezy et al. 2010) andYK7 (2) (Keyser et al. 2015)
48 [1]	*16093C 16129A* **16213A** *16223T 16298C 16327T*	C	XIO (1) (Keyser-Tracqui et al. 2003)

†Full or partial matches with the Pazyryk haplotype (PZ1) are shown in italics fonts, while any additional or missing variations are shown in bold and strike through fonts, respectively. Some mtDNA haplotypes have a wider sequence coverage reported in the literature, but only the data for the HVR1 region (16024-16365) are shown herein. Haplotypes IDs provided here are independent of those in Table 1a. Haplotypes 1 through 9 are EMPOP matches. ‡Abbreviations for the population ID's (number of samples) (reference) are the same as those provided in Table 1a, except for the following additional ones: YK1 (No.: 1 site, late 18th century CE) – Khangallassky, Yakutia Republic; YK2 (Bekh Alaas 4 site, 18th century CE) – Churapchinsky, Yakutia Republic; YK3 (Lepsei site, late 17th-18th century CE) – Verkhoyansky, Yakutia Republic; YK4 (Oyogosse Tumula II, late 18th-19th century CE) – Vilyuy, Yakutia Republic; YK5 (Balytakh site, 15th century CE) – Khangallassky, Yakutia Republic; YK6 (Alas Ebe 2, Khangallassky/Jarama 1, Churapchinsky/Ken Ebe 3, Tattinsky (2)/Orto Aryy, Tattinsky; 15th-19th centuries CE), Yakutia Republic; YK7 (Kureleekh, Verkhoyansky/Orto Aryy, Central Yakutia: pre-17th-18th centuries CE), Yakutia Republic; PZ2, Ak-Alakha-5 (Pazyryk culture, 4th-3rd centuries BCE) – Ukok, Altai Republic; PZ3, Ala-Gail-2 (Pazyryk culture, 4th-3rd centuries BCE) – Chuya Valley, Altai Republic; PZ4, Berel' (Pazyryk culture, 4th-3rd centuries BCE) – Kazakhstan; TAC, Abakano-Perevoz I (Tachtyk culture, 1st-4th centuries CE) – Bogratsky, Khakassia Republic; BTG, Baga Turgen Gol (Pazyryk culture, 4th-3rd centuries BCE) – Altai Republic; AA1, Ak-Alakha-1, mound 1, burial 2 (Pazyryk culture, 4th-3rd centuries BCE) – Ukok, Altai Republic; VK2, Verkh-Kaldzhin-2, mound 1 (Pazyryk culture, 4th-3rd centuries BCE) – Ukok, Altai Republic; ZEV, Zevakino (Zevakino-Chilikta culture, 9th-7th centuries BCE) – Kazakhstan; XIO, Xiongnu (Xiongnu culture, 3rd century BCE - 2nd century CE) – Egyin Gol Valley, Mongolia; XBK, Xiongnu (Xiongnu culture, 1st century BCE – 1st century CE) – Transbaikal, Buryatia Republic; JIN, Jinggouzi (Jinggouzi culture, 5th century BCE) – Chifeng City, Inner Mongolia, China; BAR, Barghuts – Inner Mongolia, China; KZA, Altaian Kazakhs – Altai Republic; KZX, Xinjiang Kazakh – Xinjiang, China; YUK, Yukagir – Kolyma River, Yakutia Republic; CHV, Chuvan/Chuvantsi – Chukotka, Russian Federation; NGA, Nganasans – Taymyr Peninsula, Russian Federation; AZE, Azeri – Azerbaijan; ADG, Adygei – Northwest Caucasus, Russia; YAK, Yakut – Yakutia Republic (*TTS, Tattinsky; USM, Ust-Maya; CPC, Churapcha*); UZB, Uzbek – Uzbekistan (*KHR, Khorezm*); AFG, Afghan – Uzbekistan (*DNU, Denau*); KYR, Kyrgyz – Uzbekistan (*DKU, Dzhalya-Kuduk*); TAJ, Tajik – Uzbekistan; ALT, Altaian; ALK, Altaian-Kizhi; TUV, Tuvan; BUR, Buryat; EVE, Evenki; ULC, Ulchi; ORO, Oroqen; HIM, HAN (*IMC: Inner Mongolia, China*); KAL, Kalmyk; ARB, Arab – Bahrain; KOR, Korean – South Korea; EAU, East Asian unknown – New York, USA. [1] mtDNA (HVR1) haplotypes from ancient DNA samples.

Table 2: Distributions of the language families and ethnicities of the individuals bearing full or very close Y-STR (17-loci) and/or mtDNA (HVR1) haplotype matches with those from the Ak-Alakha-1 burial site

Language Family	*Population ID* [†]	*Ethnicity*	*Number of Y-STR matches*	*Number of mtDNA matches*
Altaic: Turkic	TUR	Turkish	**5** (+9)	**3**
	AZE	Azeri	-	**1**
	KAZ / KZJ / KZA	Kazakh	(+1)	**6**
	UIG	Uighur	(+2)	**1**
	YAK	Yakut	(+2)	**10** (**+7** +8)
	CHU	Chuvash	(+1)	-
	TAT	Tatar	**1** (+3)	-
	NOG	Nogay	(+2)	-
	TMN	Turkmen	**3** (+1)	-
	UZB	Uzbek	**1** (+1)	**2**
	CHL	Chelkan	(+4)	-
	KYR	Kyrgyz	-	**1**
	ALT	Altaian	-	**13**
	TUV	Tuvan	-	**27**
Altaic: Mongolic	DON	Dongxiang	**1** (+4)	-
	MON/KHL	Mongolian/Khalkha	(+15)	**4**
	KHL/BUR/DAR	Khalkha, Buriat, Dariganga	(+1)	-
	KHL/UUL/BUR	Khalkha, Uuld, Buryat	(+1)	-
	BUR	Buryat	-	**11**
	KAL	Kalmyk	-	**2**
	BAR	Barghuts	-	**5**
Altaic: Tungusic	MCH	Manchu	(+1)	-
	EVE/EVW	Evenk	-	**22**
	ULC	Ulch	-	**1**
	ORO	Oroqen	-	**2**
Altaic: Koreanic	KOR	Korean	-	**1**
Uralic	MAN	Mansi	(+2)	**1**
	KHA	Khanty	(+13)	**3**
	YUK	Yukaghir[*]	-	**5**
	CHV	Chuvantsi	-	**1**
	NGA	Nganasan	-	**3**
Indo-European	RUS	Russian	**1** (+6)	**1**
	UKR	Ukrainian	(+1)	-
	TAJ	Tajik	**1** (+1)	**12**
	AFG	Afghan[‡]	-	**1**
Caucasian	ADG	Adygei	-	**2**
Sino-Tibetan	NHA/HAN/HIM	Han	(+2)	**2**
	HUI	Hui[§]	**2** (+2)	-
Afro-Asiatic	ARB	Arab	-	**1**
Unknown	PAZ	Pazyryk[*]	-	(**+3**+4)
	TAC	Tachtyk[*]	-	(**+1**)
	ZEV	Zevakino-Chilikta[*]	-	(+1)
	XIO / XBK	Xiongnu[*]	-	(**+2**+4)
	JIN	Jinggouzi[*]	-	(**+2**+1)
	EAU	East Asian Unknown	-	**1**
	Total		15 (+75) = 90	145 (**+15**+18)= 178

[†] Population ID's as described in Tables 1a and 1b, except for PAZ, which collectively denotes PZ2, PZ3, PZ4, BTG, AA1, AA5 and VK2. The number of full 17-loci Y-STR haplotypes are shown in bold fonts, while those with only a few allelic variations from the PZ1 haplotype are shown in brackets [for example, (+1)]. The number of full mtDNA HVR1 matches are also shown in bold fonts, while those corresponding to ancient DNA samples with full or closely matching haplotypes are shown in bold and plain fonts, respectively, and both in brackets [for example, (**+1**+1)]. [‡]Actual ethnicity and hence the language spoken by this individual is unknown. [§]Predominantly Chinese-speaking Muslims, Hui's paternal lineages are closer to those of Uighur, Mongolian and Manchu minorities in China (Zhao et al. 2017). [*]No consensus exists on the precise language family of these ethnicities.

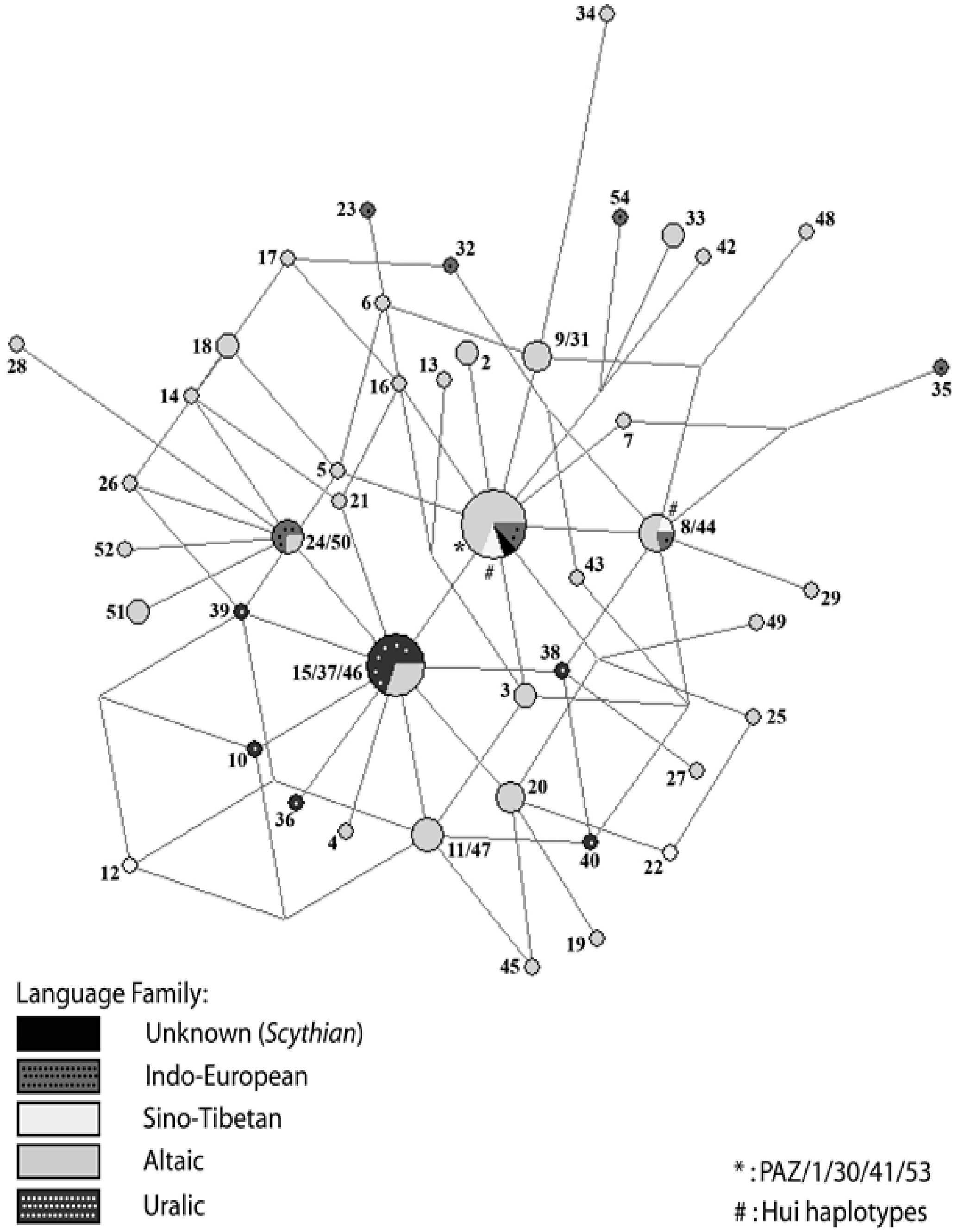

Fig. 2. M-JN analysis of the 17-loci Y-STR haplotypes corresponding to the Scythian haplotype PZ1 from Ak-Alakha-1 burial site and its contemporary matches and close allelic variants (Haplotypes 1 through 54 from Table 1a).
Source: Author

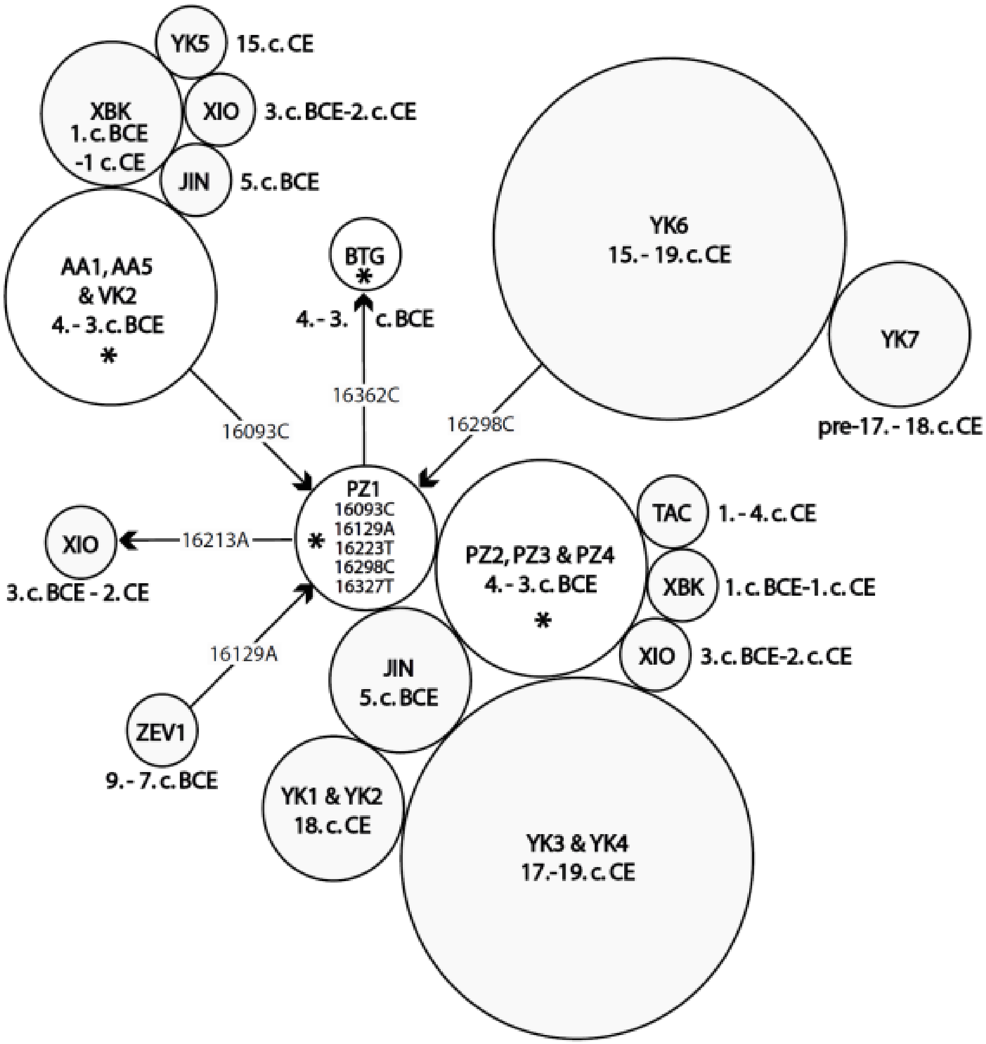

Fig. 3. A phylogenetic network for the ancient PZ1 mtDNA haplotype (HVR1) (haplogroup C) in relation to other fully matching or very closely related (only a single mutation event apart) ancient haplotypes. Each node size is proportional to the number of haplotypes reported (for example, PZ1 was observed in two individuals at Ak-Alakha-1, etc., refer to Table 1b for further details). Abbreviations for population IDs are the same as those in Table 1b. Tangential nodes denote the same HVR1 haplotype, but different populations and/or time periods and/or sites, while the arrows separating two nodes denote a single mutation event. Asterisks denote Pazyryk sample nodes.
Source: Author

ic network around the PZ1 mtDNA HVR1 haplotype, comprising full and very close variants from various archaeogenetic investigations. In the entire network, the PZ1 haplotype is the most frequent one (17 haplotypes), which is also observed in the remains from Jinggouzi, Tachhytk, Xiongnu and Yakut cultures, as well as other Pazyryk sites. The second most frequent variant (eight haplotypes) is that with only a missing mutation of 16093C, and it is observed in the remains from Jinggouzi, Xiongnu, Yakut and Pazyryk cultures. The most ancient haplotype in the entire phylogenetic network corresponds to that from the Zevakino-Chilikta culture, and differs from PZ1 by the absence of the 16129A mutation.

DISCUSSION

A recent large-scale archaeogenetic study revealed that different Scythian populations from across the Eurasian Steppe not only shared distinct cultural traditions but also strong genetic connections (Unterlander et al. 2017). This could be best explained by the presence of a substantial amount of gene flow among the ancient Scythian populations, which would also be consistent with their already known nomadic/semi-nomadic pastoralist lifestyles. Through ancient mitochondrial DNA studies, it was also shown earlier that the Altai Mountains constituted a geographical barrier for the genetic admixture of the east and west Eurasian populations up until the beginning of the Iron Age (Calafell et al. 1996; Comas et al. 1998). The beginning of the Iron Age seemingly coincided with the eastward population expansion from the Pontic-Caspian Steppe in Eastern Europe and a westward expansion of the east Eurasian populations. Indeed, archaeogenetic data on Iron Age nomad samples originating from eastern and western parts of the Eurasian Steppe suggest that the genetic composition of the ancient Scythians could be a mixture of the late Copper Age/Early Bronze Age Yamna culture and East Asian/North Siberian elements (Unterlander et al. 2017). Each ancient Scythian group was also found to bear closer genetic connections with the contemporary populations from the same region, hence indicating substantial population continuity across more than two millennia. For instance, the ancient Pazyryk people were found to share a similar mtDNA gene pool with not only the contemporary Altaians and nearby populations but also with the pre-Iron Age populations from the same region (Gonzalez-Ruiz et al. 2012).

A potential reason for the collapse of the once thriving Pazyryk culture could be attributed to the expansion of the Xiongnu people, who are credited with the formation of the first nomadic empire in Central Asia between the 2nd BCE and 1st CE. Traces of contacts between the Pazyryk and Xiongnu cultures are already evident in many respects, even in the current study, wherein both the Ak-Alakha-1 mtDNA haplotype, as well as its close variant (missing the 16093C mutation) that were observed in other Pazyryk people, were shown to be shared by ancient Xiongnu people from Egyin Gol Valley in Mongolia and Transbaikal Area in Buryatia (Fig. 2). Xiongnu are also thought to be genetically and culturally linked with the subsequent Mongolic and Turkic expansions from the same region, which could help further explain the sharing of both the Ak-Alakha-1 mtDNA and Y-STR haplotypes among contemporary populations associated with these two ethnicities (Pilipenko et al. 2018). In other words, there is an apparent population continuity from the Scythians to the Xiongnu and then onto the Turkic people, possibly because the former two already bore proto-Turkic elements. Following the collapse of the Pazyryk culture, not all members of the community disappeared, but some seemingly formed the basis of a genetic continuity with the contemporary Altaians and other nearby populations in terms of both the paternal and maternal lineages (Dulik et al. 2012; Gonzalez-Ruiz et al. 2012).

As illustrated in Figure 1, both the paternal and maternal lineages belonging to the two Scythians from Ak-Alakha-1 kurgan site exhibit clear signs of reproductive success across almost the entire Eurasian landscape and over two and a half millennia. In agreement with the results from the current study, eastern Scythian lineages were already shown to have a more widespread distribution among the contemporary populations and intriguingly almost exclusively among the Turkic-speaking populations, who are also spread over a substantial part of the Eurasian geography (Unterlander et al. 2017).

It is also noteworthy that a relatively high level of matching was observed in both the maternal and paternal lineages of the two ancient Scythians from Ak-Alakha-1 site and contemporary populations from Anatolia (Tables 1a and b, Fig. 1). This is despite the fact that the Y-chromosomal haplogroup N and mtDNA haplogroup C are today observed at their highest frequencies in both contemporary and ancient east Eurasian populations. As in the case of the Pazyryk culture, there is ample evidence for genetic admixture of the eastern and western paternal and maternal lineages in the contemporary populations from Turkey along with an overall population continuity of the original Anatolian genetic stock (Cinnioglu et al. 2004; Serin et al. 2016). For instance, the overall frequency of the Y-chromosomal haplogroup N (combined N* and N3a) was noted as only four percent across the whole country, where N* was found to account for seventy-five percent of these N lineages (Cinnioglu et al. 2004). That being said, N* alone was also shown to account for up to seven percent in Eastern Black Sea Region in Turkey, while the combined N*/N3a frequency was six percent and ten percent in the Central Anatolia and Aegean Regions, respectively (Cinnioglu et al. 2004). In the meantime, while there is still relatively limited mtDNA data available from the entire country, mtDNA haplogroup C (C4 and C4a1+16129A) was also observed with a frequency of four percent among the contemporary populations in South and Southeastern Anatolia, where haplogroups C4 and C4a1+ 16129A accounted for one percent and three percent, respectively (Serin et al. 2016). The substantial presence of the Ak-Alakha-1 mtDNA and Y-STR haplotypes in the contemporary Anatolian populations may be attributed to two major historical events: (a) the less likely being the Scythian invasion of Anatolia around 7th century BCE and settlement for around 30 years near the Aras or Araxes River (Herodotus 1920), and (b) the more likely being the Central Asiatic Turkic migrations into Anatolia from around 11th century CE onwards, keeping in mind the ever growing support for a strong genetic continuity between the ancient eastern Scythians and the proto-Turkic tribes (Unterlander et al. 2017). It should be further emphasized that, the detection in contemporary Anatolian populations of ancient Y-STR and/or mtDNA haplotypes from south Siberian cultures (for example, Xiongnu and Kurgan cultures, etc.) is by no means unprecedented and certainly not limited to those typically associated with East Eurasian populations (that is, Y-chromosomal haplogroup R1a1 and mtDNA haplogroups U4 and T1 are also shared between the both populations) (Keyser-Tracqui et al. 2003; Keyser et al. 2009; Pilipenko et al. 2018). Instead of simply disappearing upon the collapse of the Scythian culture, “the animal style” flourished over an even larger geographical domain, such as through the ethnic traditions of various Turkic peoples. Among the numerous examples are the re-appearance of the ever-popular Scythian symbolism attached with deer and deer antlers in the insignia of the Kok-Turk royal family, as well as ornamental motifs on numerous other artifacts from the associated period (Coruhlu 2014).

Traces of the Scythian influence among other Turkic people, such as those as far as from northeastern Siberia, namely Yakuts or Sakhas, were also previously proposed, but these proposals remain contested (Gogolev 1993; Savinov 2010). Recent archaeogenetic data seem to support a connection between the contemporary Yakuts and ancient Scythians, especially in terms of the Pazyryk culture, because the current model suggests that a demographic expansion of the autochthonous Altaians is more likely to account for the genetic admixture and diversity in Central Asia (Voivod et al. 2003; Gonzalez-Ruiz et al. 2012). Population genetics studies on contemporary Sakhas suggested that they have (a) rather heterogeneous maternal lineages, featuring close affinities with both the autochthonous Northeastern Siberian populations, such as Evenks, who were traditionally Tungusic-speaking reindeer-herders and hunter-gatherers and Southern Siberian Turkic-speaking Tuvans, who had a traditional economy based on semi-nomadic horse and cattle breeding (Pakendorf et al. 2003; Puzyrev et al. 2003), and (b) very homogenous paternal lineages, both geographically and chronologically, possibly due to a population bottleneck or founder effect, with an affinity to those from the Lake Baikal area (Pakendorf et al. 2006; Crubezy et al. 2010). As it can be clearly seen from Table 1b and Figure 1, the Ak-Alakha-1 mtDNA haplotype and its close variants are found abundantly among ancient and contemporary Yakuts. Furthermore, a full match at only the 12 common loci available was also observed between the Y-STR haplotype of Ak-Alakha-1 and a 15th century CE ancient Yakut, which constitutes the only match so far between the Ak-Alakha-1 haplotype and that of an ancient individual from elsewhere. It may also be added that the ornamental edge patterns on the felt hats of both ancient Scythians from Ak-Alakha-1 are also often encountered in diverse Yakut artifacts (Neustroev 1994; Polosmak 1994b; Neustroev 2010). Moreover, closer comparative analyses of the Pazyryk archaeological materials with the contemporary Siberian artifacts suggest that only those belonging to Yakuts have an unusually similar or even identical patterns with those of the Pazyryk culture (Johansen 2008).

Potential connections between the Yakuts and Pazyryk people, the latter of whom are known to have an admixed genetic character comprising both Indo-European and East Asian lineages, may also help raise the veil of secrecy over the previously proposed linguistic ties between the Yakut and Sanskrit languages (Sidorov 1997). Such an indirect link between the Yakuts and Indo-Europeans through the admixed Scythian ancestors could shed light on the inexplicable high frequency of HLA-A1, B17 genotype among the contemporary Yakuts (Fefelova 1990). Major histocompatibility complex HLA-B17 genotype is associated with a predisposition to ankylosing spondylitis (AS), or the Bekhterev disease, which is encountered with the highest frequencies among Indo-Iranians but almost absent in Mongoloids. Among Yakuts, the *HLA-B17* gene and AS is more common than in any other ethnic groups in modern Yakutia. Among the Yakut patients, gastroduodenal erosive and ulcerative lesions induced by non-steroidal anti-inflammatory drugs are encountered along with AS five times more frequently compared to non-indigenous populations (for example, Russian, etc.) (Fedotov 2011). Interestingly, the older individual from the Ak-Alakha-1 kurgan 1 was also diagnosed with AS (Polosmak 2001; Chikisheva 2003).

In response to aggressive Xiongnu expansion into the Altai region around the 2nd century BCE, some members of the Pazyryk culture may have started moving up North, and eventually reached the Vilyuy River at the beginning of 1st century CE. Notably, there is clear population continuity between the Uralic people such as Khants, Mansis and Nganasans, Paleo-Siberian people such as Yukaghirs and Chuvantsi, and the Pazyryk people even when considering just the two mtDNA and Y-STR haplotypes from the Ak-Alakha-1 mound 1 kurgan (Tables 1a, b, Table 2, Fig. 1). These concepts are also in agreement with the famous Yakut ethnographer Ksenofontov, who suggested that technologies associated with ferrous metallurgy were brought to the Vilyuy Valley at around 1st century CE by the first (proto)Turkic-speaking pioneers (Ksenofontov 1992). Yakut ethnogenesis *per se* possibly involved two major stages, the first being the proto-Turkic epoch through the arrival of Scytho-Siberian culture originating from Southern Siberia, such as that associated with the Pazyryk culture and the second being the proper Turkic epoch.

CONCLUSION

As part of an in-depth case study, extensive searches were carried out in online databases and literature for matches with the paternal and maternal lineages of the two Pazyryk individuals from the Ak-Alakha-1 mound 1 kurgan, which helped reveal a clearer picture of some of the ancient migrations across the Eurasian landscape. While the archaeogenetic data associated with the two ancient Scythians alone certainly can not be considered representative of the whole Pazyryk Culture, let alone that of the highly admixed Scythian populations at large, a rare glimpse into the genetic continuity of the two individuals from a Pazyryk Kurgan that seemingly captured contemporary human imagination was still possible. A major limitation of the current study remains the fact that despite the increasing amount of archaeogenetic data that has become available, there is still unequal data coverage on all the relevant ancient cultures and contemporary populations from across the Eurasian landscape.

RECOMMENDATIONS

Current investigation underscores the need for the generation of more population genetics data that are both spatially and geographically representative so that more authoritative conclusions on potential Scythian population continuity may be drawn.

ACKNOWLEDGEMENTS

The researchers report no conflict of interest and they are solely responsible for the content and writing of this manuscript. No particular funding was used during the realisation of this research project. The researchers thank Elena Tikhonova for her helpful comments and suggestions during the writing of this manuscript.

REFERENCES

Alekseev VP 1986. Paleoanthropology of the steppes of Eurasia in the Scythian time. In: AI Martynov, VP Alekseev (Eds.): *The History of Paleoanthropology and the Scythian-Siberian World (in Russian)*. Kemerovo: Kemerovo State University Publishing House, pp. 38-63.

Athey WT 2006. Haplogroup prediction from Y-STR values using a Bayesian-allele-frequency approach. *J Genet Geneal,* 2: 34-39.

Balanovsky O, Rootsi S, Pshenichnov A et al. 2008. Two sources of the Russian patrilineal heritage in their Eurasian context. *Am J Hum Genet,* 82: 236-250.

Balaresque P, Poulet N, Cussat-Blanc S et al. 2015. Y-chromosome descent clusters and male differential reproductive success: young lineage expansions dominate Asian pastoral nomadic populations. *Eur J Hum Genet,* 23: 1413-1422.

Bandelt HJ, Forster P, Rohl A 1999. Median-joining networks for inferring intraspecific phylogenies. *Mol Biol Evol,* 16: 37-48.

Bashilov VA, Yablonsky LT 2000. Some current problems concerning the history of early iron age Eurasian steppe nomadic societies. In: J Davis-Kimball, EM Murphy, L Koryokova, LT Yablonsky (Eds.): *Kurgans, Ritual Sites, and Settlements - Eurasian Bronze and Iron Age*. Oxford: Archaeopress, pp. 9-12.

Beckwith CI 2009. *Empires of the Silk Road: A History of Central Eurasia from the Bronze Age*. Princeton: Princeton University Press.

Calafell F, Underhill P, Tolun A et al. 1996. From Asia to Europe: Mitochondrial DNA sequence variability in Bulgarians and Turks. *Ann Hum Genet,* 60: 35-49.

Chikisheva TA 2003. Ethnogenesis of early nomads from the Altai mountains according to anthropology. In: VI Molodin (Ed.): *The Gorny Altai Population in the Early Iron Age as an Ethnocultural Phenomenon: Origin, Genesis, and Historical Destiny (Archeological, Anthropological, and Genetic Perspectives (in Russian)*. Novosibirsk: Sib. Otd. Ross. Akad. Nauk, pp. 61-120.

Chukhryaeva MI, Ivanov IO, Frolova SA et al. 2016. The haplomatch program for comparing Y-chromosome STR-haplotypes and its application to the analysis of the origin of Don Cossacks. *Russ J Genet,* 52: 521-529.

Cinnioglu C, King R, Kivisild T et al. 2004. Excavating Y-chromosome haplotype strata in Anatolia. *Hum Genet,* 114: 127-148.

Clisson I, Keyser C, Francfort HP et al. 2002. Genetic analysis of human remains from a double inhumation in a frozen kurgan in Kazakhstan (Berel site, early 3rd century BC). *Int J Legal Med,* 116: 304-308.

Comas D, Calafell F, Mateu E et al. 1998. Trading genes along the silk road: mtDNA sequences and the origin of central Asian populations. *Am J Hum Genet,* 63: 1824-1838.

Coruhlu Y 2014. *Animal Symbolism in Turkish Art (in Turkish)*. Konya: Komen.

Crubezy E, Amory S, Keyser C et al. 2010. Human evolution in Siberia: From frozen bodies to ancient DNA. *BMC Evol Biol,* 10: 25.

Cynarski WJ 2018. Propinquity of Scythians and Slavs: Remarks on the state of knowledge of Slavic ethnogenesis. *J Martial Arts Anthrop,* 18: 1-7.

Damgaard PB, Marchi N, Rasmussen S et al. 2018. 137 ancient human genomes from across the Eurasian steppes. *Nature,* 557: 369-374.

Davis-Kimball J 1995. The Scythians in southeastern Europe. In: J Davis-Kimball, VA Bashilov, LT Yablonsky (Eds.): *Nomads of the Eurasian Steppes in the Early Iron Age.* Berkeley, USA: Zinat Press, P. 27.

Denis S 1990. *The Cambridge History of Early Inner Asia*. Cambridge: Cambridge University Press.

Derenko M, Grzybowski T, Malyarchuk BA et al. 2003. Diversity of mitochondrial DNA lineages in South Siberia. *Ann Hum Genet,* 67: 391-411.

Derenko M, Malyarchuk B, Denisova G et al. 2012. Complete mitochondrial DNA analysis of eastern Eurasian haplogroups rarely found in populations of northern Asia and eastern Europe. *PLoS One,* 7: e32179.

Derenko M, Malyarchuk B, Grzybowski T et al. 2007. Phylogeographic analysis of mitochondrial DNA in northern Asian populations. *Am J Hum Genet,* 81: 1025-1041.

Di Cosimo N 1999. The northern frontier in pre-imperial China (1,500 - 221 BC). In: M Loeuwe, EL Shaughnessy (Eds.): *The Cambridge History of Ancient China: From the Origins of Civilization to 221 BC*. Cambridge: Cambridge University Press, pp. 885-966.

Di Cristofaro J, Pennarun E, Mazieres S et al. 2013. Afghan Hindu Kush: Where Eurasian sub-continent gene flows converge. *PLoS One,* 8: e76748.

Dulik MC, Zhadanov SI, Osipova LP et al. 2012. Mitochondrial DNA and Y chromosome variation provides evidence for a recent common ancestry between native Americans and indigenous Altaians. *Am J Hum Genet,* 90: 229-246.

Durmus I 2012. *Scythians (in Turkish)*. Ankara: Akcag Yayinlari.

Ercilasun AB 2008. *History of the Turkish Language from the Beginning to the 20th Century (in Turkish)*. Ankara: Akcag Yayinlari.

Fedotova AP 2011. *Gastroduodenal Erosive and Ulcerative Lesions Induced by Non-steroidal Anti-inflammatory Drugs among Residents of Yakutsk (in Russian)*. Thesis for the Medical Sciences Degree. Yakutsk: North Eastern Federal University.

Fefelova VV 1990. Participation of Indo-European tribes in ethnogeny of the mongoloid population of Siberia: Analysis of the HLA antigen distribution in mongoloids of Siberia. *Am J Hum Genet,* 47: 294-301.

Findley CV 2004. *The Turks in World History*. Oxford: Oxford University Press.

Gersdorff E, Parzinger G 2000. Radiocarbon dating of horse bones. In: AP Derevianko, VI Molodin (Eds.):

Phenomenon of the Mummies of the Altai (in Russian). Novosibirsk: Novosibirsk University, Institute of Archaeology and Ethnography, pp. 265-267.

Gogolev AI 1993. *The Yakut (Problems of Ethnic Genesis and Formation of Culture) (in Russian).* Yakutsk: Ilin.

Gokcumen O, Dulik MC, Pai AA et al. 2008. Genetic variation in the enigmatic Altaian Kazakhs of South-Central Russia: Insights into Turkic population history. *Am J Phys Anthropol,* 136: 278-293.

Gonzalez-Ruiz M, Santos C, Jordana X et al. 2012. Tracing the origin of the east-west population admixture in the Altai region (Central Asia). *PLoS One,* 7: e48904.

Grjaznov MP 1984. *Der Grosskurgan von Arzan in Tuva, Südsibirien*. Munchen: Beck.

Gubina MA, Damba LD, Babenko L et al. 2013. Haplotype diversity in mtDNA and Y-chromosome in populations of Altai-Sayan region. *Russ J Genet,* 49: 329-391.

Gubina MA, Kulikov IV, Babenko VN et al. 2016. The dynamics of the composition of mtDNA haplotypes of the ancient population of the Altai mountains from the early bronze age (3rd millennium BC) to the iron age (2nd-1st centuries BC). *Russ J Genet,* 52: 93-106.

Gurkan C, Sevay H, Demirdov DK et al. 2017. Turkish Cypriot paternal lineages bear an autochthonous character and closest resemblance to those from neighbouring near Eastern populations. *Ann Hum Biol,* 44: 164-174.

Herodotus. English Translation by AD. Godley (1920). The Loeb Classical Library. Cambridge, Massachusetts, USA: Harvard University Press.

Irwin JA, Ikramov A, Saunier J et al. 2010. The mtDNA composition of Uzbekistan: A microcosm of Central Asian patterns. *Int J Legal Med,* 124: 195-204.

Johansen U 2008. *Ornamental Art of Yakuts: Historical and Ethnographic Study (in Russian)*. Yakutsk: Dani Diamond Company.

Juras A, Krzewinska M, Nikitin AG et al. 2017. Diverse origin of mitochondrial lineages in iron age Black Sea Scythians. *Sci Rep,* 7: 43950.

Karmin M, Saag L, Vicente M et al. 2015. A recent bottleneck of Y chromosome diversity coincides with a global change in culture. *Genome Res,* 25: 459-466.

Keyser-Tracqui C, Crubezy E, Ludes B 2003. Nuclear and mitochondrial DNA analysis of a 2,000-year-old necropolis in the Egyin Gol Valley of Mongolia. *Am J Hum Genet,* 73: 247-260.

Keyser-Tracqui C, Crubezy E, Pamzsav H et al. 2006. Population origins in Mongolia: Genetic structure analysis of ancient and modern DNA. *Am J Phys Anthropol,* 131: 272-281.

Keyser C, Bouakaze C, Crubezy E et al. 2009. Ancient DNA provides new insights into the history of south Siberian Kurgan people. *Hum Genet,* 126: 395-410.

Keyser C, Hollard C, Gonzalez A et al. 2015. The ancient Yakuts: A population genetic enigma. *Philos Trans R Soc Lond B Biol Sci,* 370: 20130385.

King LW, Thompson RC 1907. *Sculptures and Inscriptions of Darius the Great on the Rock of Behistun in Persia*. London: Oxford University Press.

Kiriscioglu MF 1994. *Grammer of the Sakha (Yakut) Turkish.* Ankara: Turk Dil Kurumu.

Kong QP, Yao YG, Liu M et al. 2003. Mitochondrial DNA sequence polymorphisms of five ethnic populations from northern China. *Hum Genet,* 113: 391-405.

Kristiansen K 1998. *Europe Before History*. Cambridge: Cambridge University Press.

Ksenofontov GV 1992. *Uraanghay-sahalar. Essays on Ancient History of the Yakuts (in Russian).* Yakutsk: Yakut State Publishing House.

Lalueza-Fox C, Sampietro ML, Gilbert MT et al. 2004. Unravelling migrations in the steppe: Mitochondrial DNA sequences from ancient central Asians. *Proc Biol Sci,* 271: 941-947.

Lee HY, Yoo JE, Park MJ et al. 2006. East Asian mtDNA haplogroup determination in Koreans: Haplogroup-level coding region SNP analysis and subhaplogroup-level control region sequence analysis. *Electrophoresis,* 27: 4408-4418.

Luckenbill DD 1927. *Ancient Records of Assyria and Babylonia.* Volume II. Chicago, Illinois: The University of Chicago Press.

Macaulay V, Richards M, Hickey E et al. 1999. The emerging tree of West Eurasian mtDNAs: A synthesis of control-region sequences and RFLPs. *Am J Hum Genet,* 64: 232-249.

Mallory JP, Adams DQ 1997. *Encyclopedia of Indo-European Culture*. Chicago, London: Fitzroy Dearborn Publishers.

Malyarchuk B, Derenko M, Grzybowski T et al. 2004. Differentiation of mitochondrial DNA and Y chromosomes in Russian populations. *Hum Biol,* 76: 877-900.

Minns EH 1913. *Scythians and Greeks*. Cambridge: Cambridge University Press.

Mirabal S, Regueiro M, Cadenas AM et al. 2009. Y-chromosome distribution within the geo-linguistic landscape of northwestern Russia. *Eur J Hum Genet,* 17: 1260-1273.

Movsesian AA, Bakholdina VY 2017. Non-metric cranial trait variation and the origins of the Scythians. *Am J Phys Anthropol,* 162: 589-599.

Neustroev BF 1994. *Sakha oyuuta Mandara (Yakut Ornaments) (in Yakut Language)*. Yakutsk: Bichik

Neustroev BF 2010. *Sakha Oyuuta-bichige = Sakha Patterns and Ornaments/Mandar Uus (in Russian)*. Yakutsk: Bichik.

Pakendorf B, Novgorodov IN, Osakovskij VL et al. 2006. Investigating the effects of prehistoric migrations in Siberia: Genetic variation and the origins of Yakuts. *Hum Genet,* 120: 334-353.

Pakendorf B, Wiebe V, Tarskaia LA et al. 2003. Mitochondrial DNA evidence for admixed origins of central Siberian populations. *Am J Phys Anthropol,* 120: 211-224.

Parson W, Dur A 2007. EMPOP — a forensic mtDNA database. *Forensic Sci Int Genet,* 1: 88-92.

Pilipenko AS, Cherdantsev SV, Trapezov RO et al. 2018. Mitochondrial DNA diversity in a Transbaikalian Xiongnu population. *Archaeol Anthropol Sci,* 10: 1557-1570.

Pilipenko AS, Romaschenko AG, Molodin VI et al. 2010. Mitochondrial DNA studies of the Pazyryk people (4th to 3rd centuries BC) from northwestern Mongolia. *Archaeol Anthropol Sci,* 2: 231-236.
Pilipenko AS, Trapezov RO, Polosmak NV 2015. Paleogenetic study of Pazyryk people buried at Ak-Alakha-1, the Altai mountains. *Archaeol Ethnol Anthrop Eurasia,* 43: 144-150.
Pimenoff VN, Comas D, Palo JU et al. 2008. Northwest Siberian Khanty and Mansi in the junction of West and East Eurasian gene pools as revealed by uniparental markers. *Eur J Hum Genet,* 16: 1254-1264.
Polosmak NV 1994a. The Ak-Alakh frozen grave barrow. *Ancient Civilization,* 1: 346-354.
Polosmak NV 1994b. *Vultures: Guardians of Gold (the Ak-Alahin Kurgans) (in Russian)*. Novosibirsk: Nauka.
Polosmak NV 2001. *Ukok Horsemen (in Russian)*. Novosibirsk: INFOLIO Press.
Powell GT, Yang H, Tyler-Smith C et al. 2007. The population history of the Xibe in northern China: A comparison of autosomal, mtDNA and Y-chromosomal analyses of migration and gene flow. *Forensic Sci Int Genet,* 1: 115-119.
Puzyrev VP, Stepanov VA, Golubenko M et al. 2003. MtDNA and Y-chromosome lineages in the Yakut population. *Genetika,* 39: 975-981.
Ricaut FX, Keyser-Tracqui C, Bourgeois J et al. 2004a. Genetic analysis of a Scytho-Siberian skeleton and its implications for ancient Central Asian migrations. *Hum Biol,* 76: 109-125.
Ricaut FX, Keyser-Tracqui C, Cammaert L et al. 2004b. Genetic analysis and ethnic affinities from two Scytho-Siberian skeletons. *Am J Phys Anthropol,* 123: 351-360.
Richards M, Macaulay V, Hickey E et al. 2000. Tracing European founder lineages in the near Eastern mtDNA pool. *Am J Hum Genet,* 67: 1251-1276.
Rootsi S, Zhivotovsky LA, Baldovic M et al. 2007. A counter-clockwise northern route of the Y-chromosome haplogroup N from Southeast Asia towards Europe. *Eur J Hum Genet,* 15: 204-211.
Roux JP 1997. *'L'Asia Centrale, Histoire et Civilizations' (Central Asia, History and Civilizations) (in French)*. Paris: Fayard.
Savinov DG 2010. *Dotyurksky – the Layer in Yakut Paleo Ethnography (in Russian)*. Siberian 2 Collection. St. Petersburg: Peter the Great Museum of Anthropology and Ethnography (the Kunstkamera), Russian Academy of Sciences, pp. 68-81.
Serin A, Canan H, Alper B et al. 2016. Mitochondrial DNA control region haplotype and haplogroup diversity in South Eastern Turkey. *Forensic Sci Int Genet,* 24: 176-179.
Sidorov ES 1997. *Yakut Lexical Convergence (in Russian)*. Yakutsk: Publishing House of the Yakutsk University Press.
Stachowski M, Menz A 2006. Yakut. In: L Johanson, E Csato (Eds.): *The Turkic Languages.* London, New York: Routledge, pp. 417-433.
Starikovskaya EB, Sukernik RI, Derbeneva OA et al. 2005. Mitochondrial DNA diversity in indigenous populations of the southern extent of Siberia, and the origins of native American haplogroups. *Ann Hum Genet,* 69: 67-89.
Tarskaia LA, Melton P 2006. Comparative analysis of mitochondrial DNA of Yakuts and other Asian populations. *Russ J Genet,* 42: 1703-1711
Unterlander M, Palstra F, Lazaridis I et al. 2017. Ancestry and demography and descendants of Iron age nomads of the Eurasian Steppe. *Nat Commun,* 8: 14615.
Voevoda MI, Romaschenko AG, Sitnikova VV et al. 2000. A comparison of mitochondrial DNA polymorphisms in Pazyrik and Modern Eurasian populations. *Archaeol Ethnol Antropol Eurasia,* 4: 88-94.
Voevoda MI, Sitnikova VV, Chikisheva TA et al. 1998. Molecular genetic analysis of mitochondrial DNA or representatives of Pazyryk culture of Altai (IV-II centuries BC). *Dokl Akad Nauk,* 358: 564-566.
Voivod MI, Shulgin EO, Nefedov MV et al. 2003. Paleogenetic studies on early iron age culture from Gorny Altai (Ukok plateau). In: VI Molodin (Ed.): *The Gorny Altai in the Early Iron Age as an Ethnocultural Phenomenon: Origin, Genesis, and Historical Destiny (Archeological, Anthropological, and Genetic Perspectives (in Russian)*. Novosibirsk: Sib. Otd. Ross. Akad. Nauk, pp. 121-147.
Volodko NV, Starikovskaya EB, Mazunin IO et al. 2008. Mitochondrial genome diversity in arctic Siberians, with particular reference to the evolutionary history of Beringia and Pleistocenic peopling of the Americas. *Am J Hum Genet,* 82: 1084-1100.
Wang H, Chen L, Ge B et al. 2012. Genetic data suggests that the Jinggouzi people are associated with the Donghu, an ancient nomadic group of North China. *Hum Biol,* 84: 365-378.
Willuweit S, Roewer L 2015. The new Y chromosome haplotype reference database. *Forensic Sci Int Genet,* 15: 43-48.
Yablonsky LT 2000. Scythian triad and scythian world. In: J Davis-Kimball, EM Murphy, L Koryokova, LT Yablonsky (Eds.): *Kurgans, Ritual Sites, and Settlements - Eurasian Bronze and Iron Age*. Oxford, England: Archaeopress, pp. 3-8.
Yao YG, Kong QP, Bandelt HJ et al. 2002. Phylogeographic differentiation of mitochondrial DNA in Han Chinese. *Am J Hum Genet,* 70: 635-651.
Yao YG, Lu XM, Luo HR et al. 2000. Gene admixture in the silk road region of China: Evidence from mtDNA and melanocortin 1 receptor polymorphism. *Genes Genet Syst,* 75: 173-178.
Zeki Velidi Togan A 1981. *Introduction to General Turkish History (in Turkish)*. Istanbul: Enderun Kitabevi.
Zhao Q, Bian Y, Zhang S et al. 2017. Population genetics study using 26 Y-chromosomal STR loci in the Hui ethnic group in China. *Forensic Sci Int Genet,* 28: e26-e27.

Paper received for publication on July 2018
Paper accepted for publication on January 2019