Journal of Archaeological Science: Reports 37 (2021) 102894

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

Ancestry and identity in Bronze Age Catacomb culture burials: A meta-tale of graves, skeletons, and DNA

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ABSTRACT

After discovering the first kurgans in the steppes, the archaeologists were faced with the need to determine the social status of buried persons and the relationship between people buried within the same necropolis. Archaeology has developed its methods and criteria for assessing the social status of buried persons, such as the size of the burial kurgans, the location of burials in the center or on the periphery of the kurgan, the wealth of implements, etc. With the introduction of paleogenetic methods into archeology, new opportunities for research in this direction are opening up. The analysis of ancient DNA is a tool that allows you not to assume but to establish consanguinity.

This study presents the archaeological and molecular analysis of human remains from the East-Manych variant of the Catacomb culture. Catacomb culture dominated eastern Ukraine and southern Russia in the 3rd millennium BCE. The skeletons were recovered from kurgans of the Ergeninskii kurgan group in Kalmykia (Russia) that were radiocarbon dated the Bronze Age (25th–23rd century BCE). Y-chromosome STR analysis revealed that both individuals belonged to haplogroup R1b. This paternal lineage appears at high frequency in central, western, and northern Europe, and commonly appears among the Yamnaya. Analysis of mitochondrial DNA variation revealed the Catacomb males to belong to haplogroups H and N, respectively, both of which also appeared in the Yamnaya. These genetic data suggest a possible relationship between the Catacomb and Yamnaya cultures and contribute to our understanding of the cultural and historical processes occurring in the steppes of Eastern Europe during the Bronze Age.

1. Introduction

Paleogenetic analysis of skeletal remains from archaeological sites is changing our understanding of ancient population history. So significant are these findings that the idea of the "third science revolution in archaeology" has been seriously discussed and now openly embraced (Kristiansen, 2014; Morozova et al., 2016; Ribeiro, 2019). By combining genetics and archaeology, researchers have traced the origin of early speakers of the Proto-Indo-European (PIE) language to the territory stretching from the Urals to Northern Europe; identified the genetic profile of Early Iron Age populations in the Eurasian steppe zone, with the region extending from the Black Sea to the Altai Mountains being associated with Scythians and neighboring tribes; demonstrated genetic relationships between modern and ancient inhabitants of these areas; and uncovered the origin of the Khazars (Allentoft et al., 2015; Chekalin et al., 2019; Flegontov et al., 2016; Mikheyev et al., 2019; Stepanov et al., 2019; Triska et al., 2017; Unterländer et al., 2017). Paleogenetics has also shed light on the social organization of ancient communities, detected kinship among burials, and uncovered social relationships within families and local populations (Cassidy et al., 2020; Haak et al., 2008; Keyser et al., 2021; Mary et al., 2019).

In this regard, kurgans provide materials that are well suited for this

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https://doi.org/10.1016/j.jasrep.2021.102894
Received 3 January 2020; Received in revised form 17 February 2021; Accepted 20 February 2021

type of investigation. Understanding funerary practices and traditions is often crucial for reconstructing familial relationships and social hierarchies in such cultures. Studies of a necropolis, cemetery, or kurgan can also reveal cosmological and religious views of an ancient community. The traditions of these communities regarding the spatial orientation of the burial and observation of kinship hierarchies within the kurgan are essential for understanding social rules and religious practices (Alekshin, 1983; Alekshin et al., 1983).

The success of ancient DNA (aDNA) extraction of suitable quality depends on the degree of the preservation of the skeletons (Kornienko and Kharlamov, 2012). Due to favorable climatic and soil conditions, the anthropological material from the Caspian steppes, generally coinciding with the Republic of Kalmykia, has a higher degree of preservation than neighboring regions (Ochir-Goryaeva et al., 2018). The Caspian steppes are in Eastern European steppes stretching from the Carpathian to the Ural Mountains (Fig. 1). The high content of various salts (particularly $CaCO_3$) results in a neutral to alkaline soil pH. Carbonates and clay in soils protect human remains from the intrusion of microorganisms by forming clay or carbonaceous crust on the bones, resulting in better collagen preservation (Eckmeier et al., 2012; Fiedler et al., 2009; Reiche et al., 2003). The carbonate content in soils increases eastwards towards the Volga and the Caspian Sea, due to two main factors. First, precipitation in Europe decreases eastwards, resulting in lesser leaching. Second, there is high carbonate content in the Caspian basin's sediments. The soils in the Kuma-Manych depression are characterized by salinization, leading to increased soil pH values. These steppes have warm, dry summers and mildly cold winters with little snow (the average January temperature is – 5 degreesC, and the average July temperature is 24 degreesC). The lack of regular snow cover in winter and high temperatures in summer helps preserve the content of archaeological sites due to limited water exposure. Therefore, the human remains found in the Caspian steppes are generally suitable for aDNA analysis.

In the past, the Eastern European steppes were home to several well studied cultures. In the Pontic steppes, the Yamnaya Culture flourished between 3300 and 2600 BCE. Based on genetic data, this culture is identified with the late Proto-Indo-Europeans (PIE), making the steppes the homeland of the PIE language. Haplogroup R1b is the most common Y-chromosome paternal lineage found in both the Yamnaya (11 out of 12 studied individuals) and modern-day Western European males (Allentoft et al., 2015; Haak et al., 2015). The spread of both haplogroups R1a and R1b in Europe and West Asia has also been linked to the dispersion of Indo-European languages and the penetration of steppe ancestry to Europe (Haak et al., 2015). It has been speculated that the westward migration was primarily a male-driven process where, for every female, there were up to 15 males migrating from the steppe, although the conclusion about the sex-bias has been later challenged (Goldberg et al., 2017a; 2017b;; Lazaridis and Reich, 2017).

In addition to finding the relationships between the modern

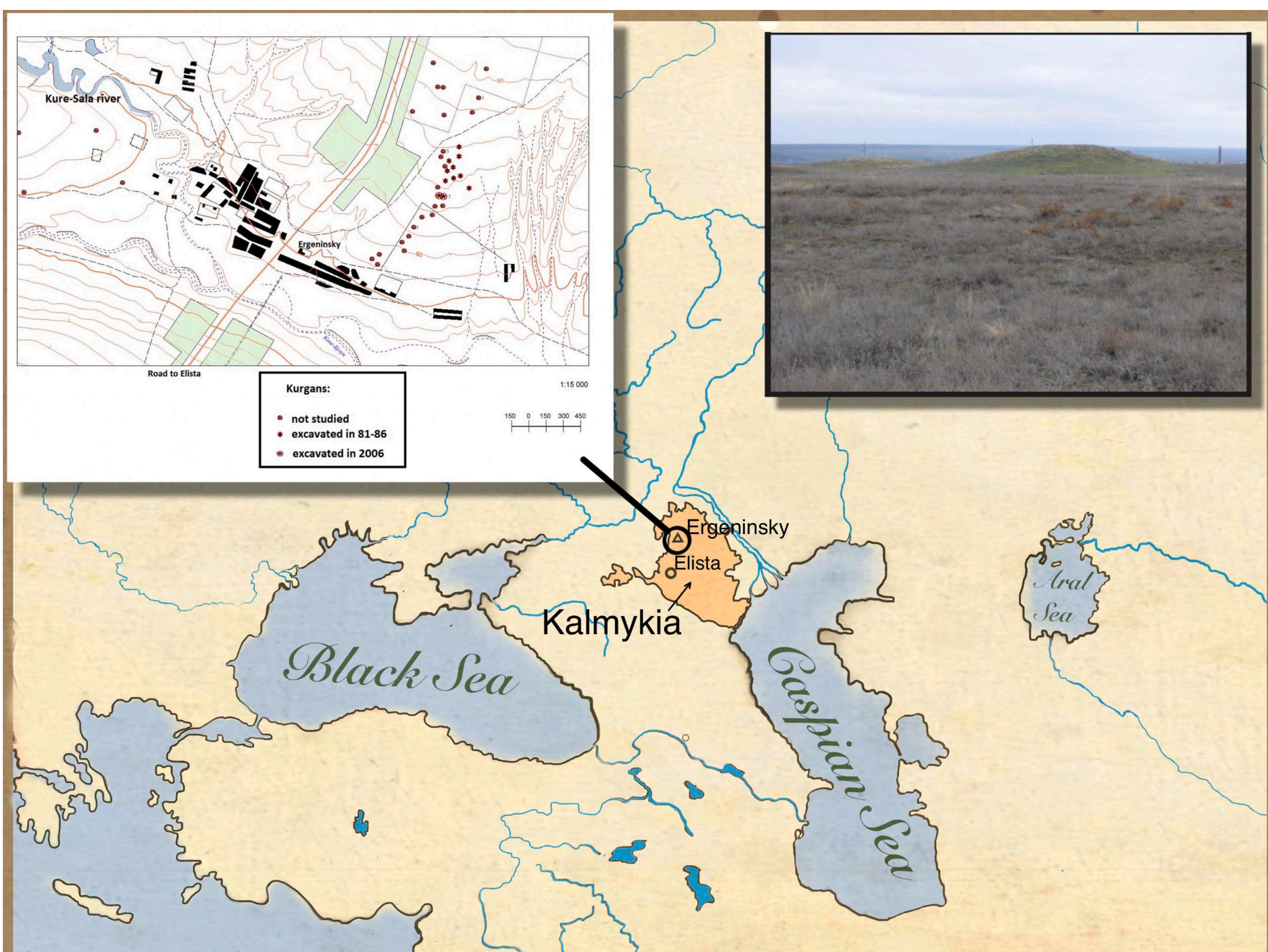

Fig. 1. Map of Kalmykia. The location of the Ergeninskii is marked as a triangle. The top-left inset shows the position of the Ergeninskii Kurgans. The top-right inset is a photograph of a typical kurgan in Ergeninskii. This is not the actual kurgan examined in this study, since these kurgans were excavated and destroyed four decades ago.

Europeans and Yamnaya, defining the relationship between the Yamnaya and the Catacomb cultures is also one of the biggest challenges of Bronze Age archaeology. According to the modern chronology based on dozens of radiocarbon analyses, the Yamnaya culture is dated to 3000–2350 BCE, while the East Manych catacomb culture is dated to 2500–2300 BCE. Several additional groups were also identified: the North Caucasian culture (2500–23500 BC), mixed Yamnaya-Catacomb and poly-ritual burials are dated to 2600–2200 BCE (Andreyeva, 2014; Shishlina et al., 2007). After the 23rd century, aridization of climate, desertification, and soil erosion in steppes (Demkina et al., 2017) facilitated the transition to nomadic cattle breeding. Items from the post-catacomb Lolinskaya culture appear in the Volga-Manych steppe also after the 23rd century BCE (Mimokhod, 2013) and can be found within the same kurgans.

Based on these details, it has been suggested that the different funerary practices reflect social stratification (Pustovalov, 2000). It is also suggested that the Catacomb people inhabited the territories left by the Yamnaya, and the two synchronous archaeological cultures living in almost sympatry (Иванова, 2009). Neither application of methods of classical archaeology to the analysis of Yamnaya and Catacomb cultures (Gey, 2009), nor the cranial series analysis (Казарницкий, 2012) were able to identify the patterns of population replacement or admixture in Early-Middle Bronze Age. Paleogenetics can offer solutions to these problems. This work is part of a large-scale study of genetic relatedness of remains buried within the same kurgan and the determination of the social hierarchy of ancient societies combining archaeological and molecular genetic analysis of paleoanthropological materials.

The paleogenetic analysis discussed in this paper is based on samples taken from the Ergeninskii group of kurgans, which have been dated to Bronze Age 2500–2300 BCE and identified as belonging to the East Manych Catacomb culture (Andreeva, 2014; Malek and Ochir-Goryaeva, 2012; Shishlina et al., 2007). The Soviet archeologist Shilov conducted excavations of the 12 Ergeninskii kurgans in 1981–1986 (Shilov, 1986, 1984a, 1984b, 1982a, 1982b, 1981) (Fig. 2).

One of the unique features of these burials is that they contained many metal artifacts among the funerary items, including knives, awls, hooks, addices, and chisels. Spectral analysis of eleven of these metal objects from Ergeninskii indicated a high brass (copper-zinc alloy) content (up to 11%), making it the earliest discovery of brass in the East-European steppes (Gak, 2004; Yegorkov et al., 2004). This discovery is significant because it modifies the traditional timeline for the earliest organized production and use of copper-zinc alloys in different human societies. The currently accepted timeline follows this specific sequence: Mesopotamia (~4500 BCE), Egypt (~3500 BCE), China (~2800 BCE), Central America (~600 CE), and West Africa (~900 CE) (Thornton, 2007).

Almost all of the currently excavated Ergeninskii kurgans belong to the East Manych Catacomb culture. All of the graves in these kurgans

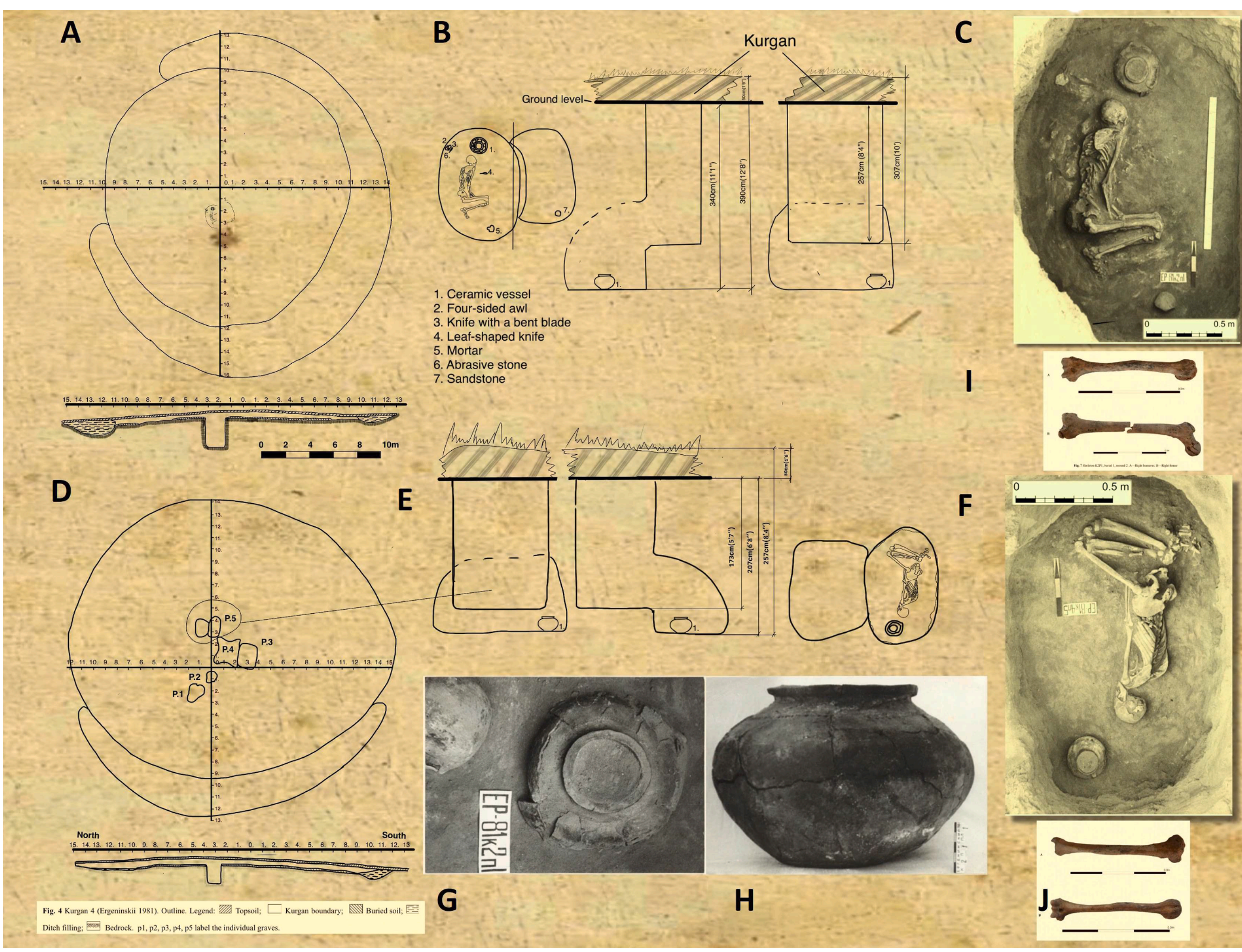

Fig. 2. Studied kurgans. A) Kurgan 2, plan (view from the top), B) Kurgan 2, profile (cross-section), C) Burial in the Kurgan 2, D) Kurgan 4, plan, E) Kurgan 4, burial 5, profile, F) Burial 5 in the Kurgan 4, G) ceramic vessel in the Kurgan 2, H) ceramic vessel in the Kurgan 4, burial 5, I) K2P1 femur bones used for DNA analysis, J) K4P5 femur bones used for DNA analysis.

(except for the four recent and two Sarmatian graves found in the same location) belong to individuals from the East Manych Catacomb culture. This fact is remarkable since the Catacomb culture did not typically construct kurgans and instead primarily reused those made by the preceding Yamnaya culture. Current estimates indicate that only 12.7% of previously discovered mounds were produced by the Catacomb culture (Andreeva, 2014). Based on these observations, we assumed that the kurgans of this group were built by a clan related by blood and kin, and the constructions were made within a relatively short chronological period, covering several generations. Two of them, Ergeninskii kurgans #6 and #11, were over five meters tall. Kurgan #11 contained one single burial under such a grandiose embankment. By contrast, three successive burials were made in kurgan #6, with each time, the embankment being filled up so significantly that each of the three graves was almost individual.

There are several remarkable features of the people who built the Ergeninskii kurgans. As mentioned above, they developed the earliest brass-making technology in Europe (Meliksetian et al., 2003). In the past, Bronze Age researchers paid little attention to reconstructions of kurgan groups or particular kurgans as mausoleums for clans and representatives of various social strata of the societies under study. Conversely, this aspect of the Scythian kurgans of the northern Black Sea coast has long been the focus of researchers and yielded exciting results about their occupants (Bunyatyan, 1985; Khazanov, 1975; Ochir-Goryaeva, 2015; 2018). For example, the social organization of the Scythians was established from an analysis of over 500 burials. A correlation was found between the social status of the deceased, the location and orientation of the burial, and the depth of the grave (Ochir-Goryaeva, 2015) (Fig. 3).

In this initial study of these kurgans, we present a molecular genetic analysis of two male skeletons from Kurgans 2 and 4. This work is part of a study on the identification of kinship and social hierarchy in ancient societies based on complex archaeological and molecular genetic analyses of paleoanthropological materials. The biological sex of the samples was initially determined by Shilov (Shilov, 1982b) at the time of excavation, although their osteological features were not carefully examined. A complete osteological description is currently impossible since, in the 40 years following the excavation, the bones were moved between laboratories and museums, thereby precluding a full examination of the complete skeletons. Thus, molecular methods were essential for accurately determining biological sex and assessing the extent of kinship between the individuals from the two Ergeninskii kurgans.

2. Materials & methods

2.1. Archeological analysis

The nomadic lifestyle of the inhabitants of the Republic of Kalmykia persisted up to the 1930th. For this reason, their anthropogenic impact on the landscape was minimal, leaving this region with a large number of well-preserved archaeological monuments. These monuments are

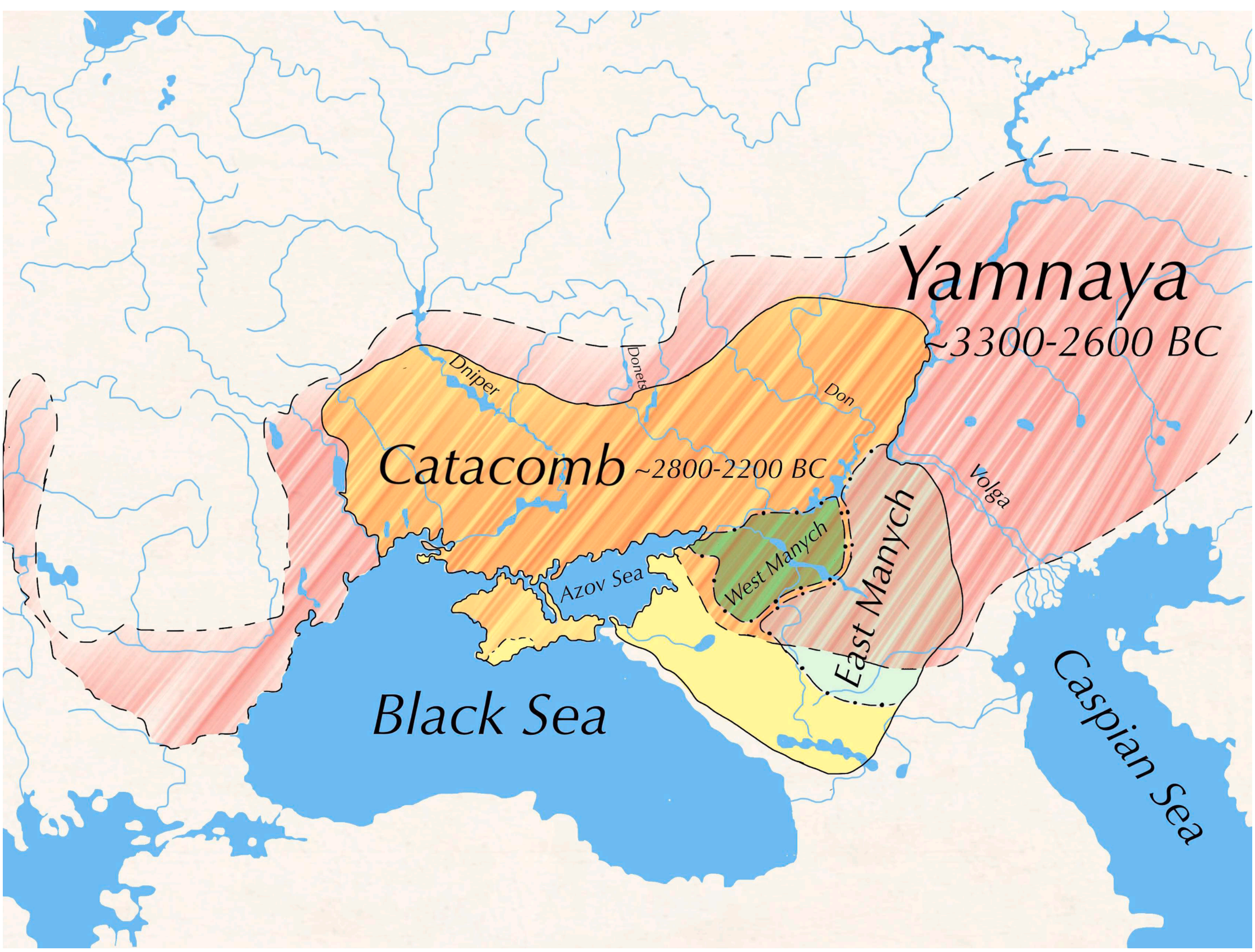

Fig. 3. Bronze age cultures of southern Russian steppes.

mainly concentrated in the valleys of rivers Shar Elsn and Kek Buluk, around the Ergeninskii village (Fig. 1). Excavations of the Catacomb culture burials on the eastern outskirts of the village were conducted by V.P. Shilov (1981-1986), and M.A. Ochir-Goryaeva and K. Malek (2006–2008). A Bronze Age settlement was excavated by M.A. Ochir-Goryaeva (2010–2012) on the western side of the village, along the banks of the Shar Elsn River. The survey has revealed six kurgan groups containing 259 kurgans within the 18 km range. The summary of the analyzed burials is given in Supplementary Table 1.

Kurgan 2 of the Ergeninskii kurgan group (Ergeninskii-1981)

Background. Kurgan 2 is located in the eastern part of the group. It is the easternmost in the chain of latitude-oriented barrows 1–3, with Kurgan 1 being in the center and Kurgan 2 positioned 35 m to the east (see map in Fig. 1). The mound of earth was slightly stretched in a north-to-south to south direction, and its eastern edge was plowed. A horseshoe-like ditch was visible in the northern, eastern, and southern sides of the kurgan. There was a bridge across the moat in the western sector of the barrow. The ditch was, on average, 3.0–4.5 m wide and 0.25 m deep; 0.21 m deep along the west-east line and 0.50 m deep from the buried soil level. No artifacts were recovered in the soil of the mound.

*Profile of Kurgan 2 (Fig. 2**A**, Supp. Fig. 1, and Supp. Table 1).* The profile of this kurgan was examined along the north-to-south line on its eastern side. Its upper layer was formed by modern turf, some 0.10–0.15 m thick. The buried soil level was registered at a depth of 0.50 m from the zero-reference point; it was easily traced in the northern part of the profile between the markers of 7.60 m and 10 m to the north but much less clear between 6 m and 9 m to the south. This level was 0.10–0.07 m thick. Between the markers of 1.50 m and 3.25 m to the south, the buried soil was interrupted by a hollowed-out space off the main shaft (with an entrance); its bottom was traced at a depth of 3.28 m to the zero-reference point. On both sides of the kurgan, there were ditches 3.0–4.5 m wide and 0.30–1.00 m deep to the buried soil level. The earth mound was homogeneous without any additional material.

The burial pit (grave 1) in Kurgan 2 (Fig. 2**B and 2C and Figs S2, S3**) was discovered on the border of the south-eastern and north-western sectors, between the markers of 1.50 m and 3.20 m to the south from the central benchmark. This pit was rectangular (1.73 m × 1.10 m) with rounded corners and dug in a north-northwest to south-southeast orientation. The depth was 2.57 m, measured from the level of the buried soil. In the western wall of the pit, there was a catacomb. The catacomb had a step of 0.73 m in height. In profile, it had a rounded shape and was 2.05 m long and 1.47 m wide; its bottom was at a depth of 3.40 m from the level of the buried soil.

The adult male skeleton was located at the bottom of the pit. It was placed on its left side in a semi-fetal position, its head oriented towards the north-west. The face was turned to the east and tilted down. The right clavicle and scapula had collapsed on the sternum. The arm bones were stretched along the body and were slightly bent at the elbows, with the hands being placed between the thighs. The left hand was positioned in front of the right. Symmetrically positioned leg bones were bent at the knees. The feet were located almost perpendicular to the tibia, with toes turned southwest. The estimated height of the buried individual is ~ 176 cm (Table 5).

There were numerous funerary items in the grave: (1) Hand-molded ornamented black clay vessel. The maximum diameter is 30 cm, the rim diameter is 15.5 cm, the height is 18.6 cm, and the bottom diameter is 12–12.5 cm. The rim is sharply bent outward. Found near the northern wall of the pit, behind the skull. (2) Bronze tetrahedral awl. The length of the preserved part is 4.41 cm, the width of the edge is 0.3 cm, an awl with the remains of a wooden handle. Found in the northwestern corner of a pit near the walls. (3) Bronze ax-shaped knife, single-edged and sharpened from the back in the front of the blade. Dimensions: length 8.8 cm, width 2.4–1.6 cm, length of the petiole 3.8. Found near an awl. (4) Bronze leaf-shaped knife with a handle; the length of the preserved part is 9 cm, the length of the handle is 5 cm, the width is 2.8–1.5 cm, the knife is double-edged. Found near the humerus, perpendicular to them, the point directed eastward. (5) Fragment of a stone mortar with a depression. The mortar is made of solid dark colored stone. Dimensions: 14x13x4 cm. Found in the southeastern corner of the pit. (6) Grinding stone, abrasive sandstone. Dimensions: 5.5x8x3 cm found next to an awl and a knife. (7) Sandstone. Dimensions: 9.5x8x3 cm. Found in the entrance pit in the southeastern corner. Traces of dusting (possibly, chalk) were found around the skeleton at the bottom of the catacomb.

Kurgan 4 of the Ergeninskii kurgan group (Ergeninskii 1981)

Background. The earthen mound had an oval shape that stretched slightly along the west-east line. Its diameter was 23 m along the north–south direction and 27.5 m along the west-east line; it rose to 0.50 m from the buried soil level. A ditch was found in the southern, southwestern, and south-eastern sides. It was 1.5–3 m wide and 0.40 m deep from the buried soil level. No finds were recovered in the earth of the kurgan.

Profile of Kurgan 4 (Fig. 2***D* and *Fig S4***). The profile of this kurgan was examined along the north–south line on the western side. Its upper layer was formed by modern turf 0.10–0.15 m thick. The level of buried soil was registered at a depth of 0.50 m from the zero-reference point. The buried soil layer was 0.07–0.10 m thick; the soil was light yellow. The mounded earth consisted of loam with whitish impregnations of the carbonate layer. In the southern part, there were traces of a ditch, 3 m wide and 0.40 m deep from the level of the buried soil.

*Burial pit (grave 5) and skeletal material in Kurgan 4 (Fig. 2**D, 2E, and Fig S5, S6**).* The grave was located on the border of the kurgan north-western and northeastern sectors of the kurgan. The shape of the grave spot was trapezoidal, with rounded corners. The long axis of the pit was oriented along a north–south line. The western wall was 1.40 m long, and the eastern wall was 0.85 m long; the width of the inlet pit was 1.14 m. The walls of the pit were sheer; the bottom was even located at a depth of 223 cm from the zero-reference point. In the eastern wall of the entrance pit, there was an additional catacomb. The catacomb had a nearly oval shape, oriented with its long axis along the north–south line. The catacomb was 2.63 m long and 1.04 m wide. Its arch was registered at a depth of 1.83 m from the zero-reference point. There was a 28 cm high step from the entrance pit to the catacomb. The bottom of the catacomb was at a depth of 257 cm from the zero-reference point.

At the bottom of the burial was positioned a skeleton of an adult male. It was placed on its left side with knees bent (Fig. 2**F**). It was oriented along the north-to-south line, with the head turned to the south, leaving the face turned east and tilted downwards. The bones of the arms were stretched along the body, with the hands placed between the thighs. The skeleton collapsed onto the chest so that the bones of the left hand were under the chest and the pelvis was slightly turned down. The leg bones were bent 15 degrees at the hips and 30 degrees at the knees. The feet bones were perpendicular to the tibia, with toes turned towards the north-east. The estimated height of the buried individual is ~ 170 cm (Table 5).

A single black clay molded vessel, pear-shaped with a side handle, was found to the right of the skull in the southwest corner of the catacomb.

2.2. DNA analysis

2.2.1. Sample preparation and DNA extraction

The right humerus and right femur from skeleton K2P1, burial 1 of mound 2 (Fig. 2**I and** S7), and the left tibia and right humerus from skeleton K4P5, grave 5 of mound 4 (Fig. 2**J and** S8), were selected for DNA analysis. The long bone samples were used for ancient DNA extraction using the methods of (Kornienko and Kharlamov, 2012). This method uses a proprietary lysis solution that gently eliminates the contamination of archaeological samples with modern DNA.

2.2.2. Autosomal DNA diversity

Both samples were surveyed for sequence variation at some autosomal DNA loci (*D3S1358, TH01, D12S391, D1S1656, D10S1248, D22S1045, D2S441, D7S820, D13S317, FGA, TPOX, D18S51, D16S539, D8S1179, CSF1PO, D5S818, vWA, D21S11, SE33*) and screened for biological sex using *Amelogenin* locus using the COrDIS-Expert kit (Gordiz, Russia). To assess the specificity of the amplification reactions, a positive control (MK1 from COrDIS-Expert kit) was used. The amplicons were run on an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems, USA). Data from these loci were collected and processed by Run 3130 Data Collection (v.3.0) software, and the identification of alleles was made using Gene Mapper ID (v.3.2) software. Allele sizes were scored against the S450 size standard concerning the allelic leader attached to the COrDIS Expert kit.

2.2.3. Y-chromosome diversity

Y-STR analysis. Besides, the samples were genotyped for Y-chromosome microsatellite loci present in the COrDIS-Y kits (Gordiz, Russia) (*DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385a, DYS385b, DYS438, DYS439, DYS437, DYS447, DYS576, DYS449, DYS456, DYS448, and DYS635*) and AmpFlSTR Yfiler PCR Reagents (Applied Biosystems, USA) (loci: *DYS456, DYS389I, DYS390, DYS389II, DYS458, DYS19, DYS385a, DYS385b, DYS393, DYS391, DYS439, DYS635, DYS392, YGATA H4, DYS437, DYS438, DYS448*). Positive controls (MK1 from COrDIS-Expert kit and 007 from AmpFlSTR Yfiler PCR Reagents) were used to assess the specificity of the amplification reactions. The amplified Y-STR loci were run on the ABI PRISM 3130 and data collected and processed as described above. Alleles sizes were identified using S450 and LIZ500 standards in the COrDIS-Y and AmpFlSTR Yfiler kits, respectively.

Y-SNP Genotyping. The Y-chromosome samples were screened for the M343 biallelic marker (position 3019783, C/A) to check whether they belonged to haplogroup R1b. SNP typing was performed using the ABI PRISM SNaPshot Multiplex Kit (ThermoFisher Scientific), and the amplicons run on the ABI PRISM 3130xl Genetic Analyzer, as described above.

Haplogroup Status. The haplogroup of the identified Y-STR haplotypes was determined using the Y-chromosome haplotype reference database (YHRD, https://yhrd.org) (Willuweit et al., 2007). The paternal lineage of these individuals was also evaluated using the online Haplogroup Predictor program (http://www.hprg.com) (Athey et al., 2006), which among other analogs, most accurately predicts the haplogroup of the Y chromosome according to the typing results of polymorphic Y-STR loci (Emmerova et al., 2017).

The probability of the haplotype belonging to the same paternal line was calculated according to the formula: $W = \frac{1}{1+\frac{1}{LR}} \times 100\%$, where LR (likelihood ratios, LR $= 1/p$, where p – the frequency of the haplotype according to the YHRD base) shows the relation of the probability of the event that this group is a related group to the likelihood of the event that the identified object is not related to this group, but randomly approaches it according to its DNA profile.

2.2.4. Mitochondrial DNA analysis

The samples were screened for SNP markers defining haplogroups A, B, C, D, E, F, G, H, I, L1 / L2, L3, M, N, and X using a multiplex PCR and SNaPshotReady Reaction Mix test kit, following the protocol of Nelson et al. (2007). These markers included the 8272–8280 del and the following SNPs: A663G, G1719A, C3594T, A4833G, C5178T, C7028T, C7600T, A10398G, C10400T, A12308G, T12312C, G12406A and A13263G (nucleotide changes are based on the revised Cambridge Reference Sequence (Andrews et al., 1999). The absence or presence of the A12308G SNP that defines haplogroup U was also determined by direct sequencing of the np 12,224–12,338 region in the mtDNA genome. See supplement for details of this analysis.

2.2.5. Height determination

The lengths of the long bones of the examined skeletons were measured, and then several approaches were used to reconstruct the heights of the buried individuals. We used the following methods (Table 5): unconditional method of Trotter and Gleser (Trotter and Gleser, 1952) and conditional on the ethnicity (Trotter and Gleser, 1952) assuming known ethnicity and gender of samples; Dupertui and Hedden (Dupertuis and Hadden, 1951); Nainis (Nainis 1966); (6) Lorke, Munzner and Valter (1953); (7) Pashkova (Pashkova, 1963) assuming known gender.

3. Results

3.1. Archaeological analysis

The Ergeninskii kurgans are arranged in several chains with an orientation along the line northeast to the southwest. One of these chains was formed by kurgans numbered from 1 to 4. Kurgan 2, from which the K2P1 sample was taken, was the second kurgan from the east. Kurgan 4, from which the K4P5 sample originated, was the last on the western side of the chain. The median axis of the kurgans of the Yamnaya and Catacomb cultures was positioned along the northeast-southwest line. In these cultures, the northeast was associated with the forward direction and the southeast in the backward direction; also, the right-hand side was associated with the east, and the left-hand side was west (Ochir-Goryaeva, 2018). Accordingly, those burials placed in the eastern and northeastern direction seemed to be more important than those who were placed in the western and southwestern direction (Ochir-Goryaeva, 2018; Очир-Горяева and Малек, 2011). Therefore, the individual from Kurgan 2 was assumed to be higher in the social hierarchy than the individual from Kurgan 4.

Both burials were primary and first in their kurgans, with the earthen mounds being initially heaped above these primary graves. The kurgans were similar in size, rising to 0.50 m; their diameters were in the range of 23–27 m. These dimensions suggested that an equivalent amount of labor was required for their construction. Notably, the grave in Kurgan 2 was singular, with no other burials in this kurgan. This might be another indicator of a higher social status and a special tribute to the one who deserved a personal kurgan. By contrast, Kurgan 4 contained multiple burials, including the individual K4P5. The entrance pits leading to the catacomb chambers, as well as the catacombs themselves, did not differ much as far as the sizes of the burials in question are concerned. The entrance pit to the burial in the kurgan 2 was bigger (173 × 110 cm) compared to the burial from the Kurgan 4 (140 × 114 cm). And the dimensions of the catacombs were 205x147 cm (Kurgan 2) and 268x104 cm (Kurgan 4). The principal difference between the two was the depth of the burial pits. In kurgan 2, it was 340 cm from the buried soil level, and in Kurgan 4, it was 207 cm. Therefore, there was over a meter difference in depth between the two burials.

This finding warranted special notice, because in some archeological cultures, the depth of burial pits had a direct association with the social status of the buried humans. In fact, there seems to be a regular pattern associated with this parameter. To illustrate, male graves tended to be deeper than those of females, graves for adults were always deeper than children's, as well as those of servants, were the least deep of the graves (Ochir-Goryaeva et al., 2018).

Of further importance were the differences in the funerary items in the two burials. The buried male in kurgan 2 was provided with more numerous and more prestigious items, including besides a vessel, decorated with an ornament, a number of bronze tools (a tetrahedral awl, an ax-shaped knife; a leaf-shaped knife) and a number of stone utensils (a fragment of stone mortar with a hole, a grindstone, an abrasive stone and a sandstone). By contrast, his counterpart from Kurgan 4 was buried with only one item, a vessel with a geometric ornament. Therefore, it seems that the two males of Kurgans 2 and 4 came from the same clan but differed in social status.

3.2. Genetic analysis

The two Ergeninskii skeletons were confirmed to be males through analysis of the amelogenin locus. The study of autosomal microsatellite loci produced a consistent genotyping result for both skeletons at only nine autosomal STR loci due to the low concentration of DNA recovered from them (Table 2). A comparative analysis of the autosomal microsatellite loci showed four of them (TH01, D12S391, D18S51, vWA) to have mismatches in allelic pairs (Table 2). For a father-son relationship to be possible, all of the loci needed to have at least one matching allele. Therefore, K2P1 and K4P5 skeletons were not first-degree relatives.

Analysis of Y-STRs in the K2P1 and K4P5 individuals agreed at 8 out of 9 loci (DYS456, DYS389I, DYS385a, DYS385b, DYS393, DYS391, DYS437, DYS448) (Table 3). These data suggested that they might be (distantly) paternally related to each other. The TMRCA estimate for the two Y-STR haplotypes was 19.6 generations (95% confidence interval 4.7 to 109.2 generations). The worldwide frequency of this overlapping eight-locus Y-haplotype (indicated by green color in Table 3), calculated using the online YHRD base (Willuweit et al., 2007), was 292 matches in 261,122 haplotypes. This is approximately 1 match in 894 haplotypes (95% CI: 1 in 1,006–1 in 797) (as of 02/16/2021). In addition, the probability of K2P1 and K4P5 belonging to the same paternal lineage was estimated to be 99.875%.

SNP genotyping with the R1b defining mutation M343 (C → A) revealed that both individuals had this mutation. Haplogroup R1b is commonly observed among contemporary European populations and appears at low frequencies in Asia and Africa (Myres et al., 2011). In addition, R1b Y-chromosomes predominate among the representatives of the Early Bronze Age Yamnaya culture in Eastern European steppes (14 out of 15 currently analyzed Yamnaya individuals; see Table S1). R1b has not been found in samples from Caucasus (Wang et al., 2019). Moreover, the dispersal of R1b has been associated with the spread of Indo-European languages (de Barros Damgaard et al., 2018; Haak et al., 2015).

The results of the mtDNA SNP analysis are shown in Table 4. The mtDNA of K2P1 belonged to haplogroup H, and that of K4P5 to haplogroup N. Haplogroups N and H appeared in the Near East and spread to Europe and the Caucasus during Neolithic expansions (Brotherton et al., 2013; Wang et al., 2019). Both haplogroups were also found in the Steppe and Caucasus samples (Sokolov et al., 2016; Wang et al., 2019). Haplogroup H originated in West Asia approximately 20,000 years ago and is currently distributed all over Europe (Roostalu et al., 2007), Haplogroup N is approximately 55,000 years old, and its derivative lineages are distributed all over Europe and Asia (Tanaka et al., 2004). Haplogroups H and N were also previously found among Yamnaya individuals (Haak et al., 2015). To determine the finer subclades to which these mtDNAs belong, additional sequencing will be needed. Details of the molecular-genetic analyses are described in the Supplement (Tables S2-S9, Figs. S1-S4).

4. Discussion

The genetic similarity between the Yamnaya and modern Europeans is evident in the prevalence of R1b haplogroups in both populations and the replacement of the original European paternal lineages by R1a and R1b after the westward migration of the Yamnaya; autosomal SNP data suggest this, as well (Bălănică et al., 2020; Lamnidis et al., 2018; Ning et al., 2019). Yamnaya people used their relatively advanced technology and mobility to sweep across Europe (Brace et al., 2019; Olalde et al., 2019). Archeological evidence attests to the impact of the spread of the Yamnaya people in terms of lethal injuries left on the skeletons of local populations (Meyer et al., 2009), and different burials practices for men compared to women (Bourgeois and Kroon, 2017). Several generations after the conquest, all of the men would possess Y-chromosomes characteristic of Yamnaya, strongly indicating that only the Yamnaya men fathered children in the conquered communities (Brace et al., 2019;

Table 1
Locus-specific mutation rates.

Locus	DYS19	DYS385a	DYS385b	DYS389I	DYS389II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	DYS447	DYS448	DYS449	DYS456	DYS458	DYS635	YGATA H4
Mutation rate	0.0017	0.0035	0.0035	0.0035	0.0087	0.0052	0.0017	0.0017	0.0017	0.0013	0.0007	0.0069	0.00264	0.0017	0.0156	0.0017	0.0087	0.0017	0.0017

Table 2
Comparative molecular genetic analysis of autosomal STR loci (NA = missing data). Color coding: yellow - comparison cannot be made due to missing data; green - possible first-degree relationship; brown - impossible first-degree relationship.

Locus	K4P5	K2P1
D3S1358	16,17	15,16
TH01	8,9.3	9,9
D12S391	21,22	24,24
D2S441	11,11.3	11,11
D7S820	7,10	9,10
D18S51	12,16	13,13
vWA	16,16	20,20.1
FGA	21,24	NA
TPOX	8,11	NA
D16S539	NA	11,11
D21S11	NA	29,29

Table 3
The results of the study of STR loci of the Y-chromosome of the samples. NA indicates the absence of amplicons. Color coding: yellow - comparison cannot be made due to missing data; green - match; brown - mismatch.

Locus	Skeleton K4P5	Skeleton K2P1
DYS456	16	16
DYS389I	13	13
DYS390	24	–
DYS389II	–	28
DYS458	16	–
DYS19	14	–
DYS385a	11	11
DYS385b	14	14
DYS393	12	12
DYS391	11	11
DYS439	12	13
DYS635	23	–
DYS392	14	–
YGATA H4	–	13
DYS437	15	15
DYS438	12	–
DYS448	19	19
DYS447	25	–
DYS449	29	–

Olalde et al., 2019).

In spite of growing knowledge about the Yamnaya culture, the linkage between the Yamnaya and Catacomb cultures is still debated (Lichardus-Itten and Lichardus, 2018). The limited number of Catacomb samples analyzed for genetic variation does not yield population-level data, and this culture also occupied a much smaller territory compared to the Yamnaya. Certain autosomal and mtDNA studies also did not find a close genetic similarity between the Yamnaya and Catacomb cultures (Pashnick, 2014). In addition, based on osteological evidence, the Yamnaya people were tall and had dolichocephalic crania (the average male was 175.5 cm in height) (Haak et al., 2015; Mathieson et al., 2015; Wilde et al., 2014), while the representatives of Catacomb culture were stockier and had more brachycephalic crania. According to the interpretation of craniological data (Khudaverdyan, 2011, 2012), the Catacomb culture skulls supposedly showed Mediterranean features, indicating their possible migration into the region from the Armenian Highland and the Caucasus.

Generally, representatives of Catacomb culture used the existing Yamnaya (as well as older) kurgans to bury their dead. However, one obvious difference in funerary practices between the cultures is the shape of the burial chamber. The Yamnaya culture used rectangular graves, while the representatives of Catacomb culture usually added a catacomb - a side chamber next to the grave. The cardinal orientation of the kurgan and the system of kurgans is the same for the Yamnaya and Catacomb cultures, where the system of kurgans formed chains in the Northeast to Southwest or Northwest to Southeast direction. Another difference is the placement of the body in the grave. The Yamnaya laid their dead on their backs with knees bent upwards, whereas the East Manych Catacomb culture buried them on the left side in a semi-fetal position.

Yamnaya preferred the Pontic steppes with their abundance of rivers and rich fertile soils. This ecological preference allowed the Catacomb culture to flourish within the broader horizon of the Yamnaya. The density of the burial sites of the Yamnaya culture increases from east to west, from more severe natural conditions to more favorable. In the Southern Urals there are 394 pit burials (Morgunova, 2014); in the Caspian steppes, 660 burials (Ochir-Goryaeva, 2008), in the Lower Don region, 1,050 burials (Faifert, 2018); and, in the Northwestern Black Sea region, 2,500 burials of the Budzhak pit culture (Ivanova, 2015, 2013). Around 80% of the kurgans found in the Pontic steppes, including the large kurgans up to 15 m tall, were built during the Yamnaya period. Therefore, there were more Yamnaya than Catacomb burials during that time (Черных and Дараган, 2014).

The Caspian steppe is now an arid zone of eroded karst limestone. However, starting 14,000 years BCE, this area went through a series of transformations. During the post-glacial period, the Caspian Sea grew to an enormous size due to the influx of glacial meltwater and eventually spilled into the Azov Sea via the Manych spillway. Around 6,000–7,000 BCE, the Black Sea basin also flooded and connected with the Mediterranean Sea to the extent that it was colonized by marine animals. The water levels eventually stabilized, and continued climate warming dried up the spillway, turning it into a series of lakes surrounded by steppes, while the Black Sea retreated to its former size (Balabanov, 2007; Giosan, 2007; Ryan and Pittman, 1998). It has been speculated that the sequences of Caspian-Black Seas floods have initiated a chain of significant migratory events in the history of Europe. After the flood era, the steppe societies went through the Neolithic revolution, transitioning from a hunter-gatherer lifestyle to one of agriculture and settlement, thereby making an increasingly larger population possible.

Representatives of East-Manych Catacomb culture built their own kurgans, were expert bronze smiths, had established settlements, and manufactured animal-driven wheeled wagons (Anthony, 2010). They were able to travel longer distances compared to the Yamnaya and had a more diverse diet (Gerling, 2015; Pokutta, 2017; Shishlina et al., 2014; Ventresca Miller et al., 2014). Analysis of the artifacts from Catacomb burials also indicates material exchanges between the representatives of Catacomb culture and Caucasus agriculturalists (Andreeva, 2014; Kohl, 2007; Shishlina, 1997). A reliable indicator of the successful economic development of the Catacomb culture in the Caspian steppes is that the number of burials of the Catacomb culture is more than twice higher than of the Yamnaya. Analysis of funerary items from the Ergeninskii kurgans further shows that the representatives of East-Manych Catacomb culture had mastered bronze work. In fact, the Ergeninskii kurgans contain multiple bronze items (knives, awls, hooks, adzes, and chisels) and even the oldest brass in Eastern Europe.

The Catacomb culture emerged on the Pontic steppe between 2800

Table 4
mtDNA SNPs and haplogroup determination.

SNP Sample	8272-8280del	13,263	1719	5178	663	10,398	10,400	3594	7028	12,308	12,312	12,406	4833	7600	resulting mt Haplogroup
K2P1	C	A	G	C	A	A	C	C	C	A	C	G	A	G	H
K4P5	C	A	G	C	A	A	C	C	T	A	C	G	A	G	N

Table 5
(1) Method of Trotter and Glazer (1952) does not take ethnicity information into account. (2) Method of Trotter and Glazer (1958) and Alexeev (1966) assumes the samples to be Caucasian origin males. (3) Dupertui and Hedden (1951). (4) Dupertui and Hedden using long bones. (5) Nainis (1966). (6) Lorke, Muncner and Valterv (1953). (7) Pearson (Pashkoa 1963), (8) Manuvrie (1892), (9) Rolle, 1888. (10) Tel'aka, 1950.

Sample	Bone	Length in cm	1	2	3		4		5		6	7		8	9	10
Kurgan 2	Left shoulder	35.9	181	181.75	178.574	178.7088	178.933	177.5298	175.3226 ± 9.78 174.5	176.8343 ± 8.64	178.4547	174.5356	174.4543	178.14	> 180	177.75
	Right femur	48.7	177.25	178.5	178.837		176.8196		176.4939 ± 8.85 175.4		176.1746	172.862		174.6	> 180	176
Kurgan 4	Left femur	35.8	168.75	168.5	169.4784		166.0616		No data	166.2024	168.6282	163.7248		164.57	162.4	168.6
	Right shoulder	34.0	175.25	176.3	167.451		173.29		169.976 ± 9.78	172.502	169.037			169.7	173	172.5

and 1700 BCE, most likely as an outgrowth of the Yamnaya culture, whose territory the Catacomb culture largely absorbed. Thought to be Indo-European speaking, the Catacomb culture expanded south and north in the region, in the process influencing the Poltavka culture in the Volga-Ural steppe (Anthony, 2019). While there are subtle genetic differences between the Catacomb and Yamnaya cultures, there seems to be general continuity of mtDNA lineages among Pontic steppe populations extended back to at the Bronze Age. However, these genetic influences did not fully extend south into the North Caucasus. Ancient DNA data indicate that members of the Early Bronze Age Maykop culture (3700–3000 BCE) were genetically distinctive from steppe populations dating to the same period, including the Yamnaya (Wang et al., 2019). By contrast, individuals from Catacomb and Yamnaya cultures were genetically similar to individuals from North Caucasus cultures. Thus, while the major expansion of steppe pastoralist and related groups seem to have culturally influenced the Maykop people, the Maykop tend to show stronger ties to cultures to the south and west of the North Caucasus (e.g., Iran, Azerbaijan) (Kuz'mina, 2007).

Due to the small sample size, we cannot "prove" the connection between the East-Manych Catacomb and Yamnaya cultures. However, our results do not rule out that such a connection may exist. The two males have haplogroup R1b Y-chromosomes and haplogroup H and N mtDNAs, respectively. Both paternal and maternal lineages were common among Yamnaya individuals and in modern European populations (see Supplemental Table 10). While this pattern may be a result of matings between Catacomb females and Yamnaya males, our mtDNA analysis does not rule out the possibility of matrilineal relatedness between the Yamnaya and representatives of the East Manych Catacomb culture. Therefore, it appears more plausible that the representatives of the East Manych Catacomb culture descended from Yamnaya by means other than force.

In addition, we have investigated the potential paternal kinship between the two individuals. They show genetic relatedness at the level of distant blood relatives. The male from Kurgan 2 also had a personal mound of earth and was buried in a deep grave chamber with valuable tools of bronze and stone, suggesting he had high social status. By contrast, the male from "communal" Kurgan 4 was buried in a shallow grave with few grave goods at the less prestigious western end of the kurgan chain. Thus, two males of Kurgans 2 and 4 differed in their social status, although possibly also belonging to the same clan. Future genetic analyses of other burials from Catacomb kurgans will further delineate the extent of kinship and clan identity among them.

5. Conclusions

Our study confirmed the existing assumption that the Ergeninskii kurgan group was a necropolis of a consanguineous group of humans. Investigation of other necropolises of the Caspian steppes will show whether this was a common practice for the Catacomb culture. Our findings also suggest that one of the people had higher social status and was buried in an individual kurgan. We have determined that the two analyzed Catacomb culture representatives were male, they both had R1b Y-DNA haplogroup, and H and N mtDNA haplogroups, suggesting possible relatedness both with Yamnaya people as well as modern Europeans. These findings help to complete the picture of cultural and historical processes in the steppes of Eastern Europe at the turn Middle and Early Bronze Ages.

Acknowledgments

We are grateful to Mr. Michael Christie for assistance with illustrations. Molecular genetic analyses and archeological research were part of the work on the implementation of the state assignment project (no. 01201363186), Federal Research Center, Southern Scientific Center of the Russian Academy of Sciences, Rostov-on-Don, Russia, 344006 and was funded by government grant "From Paleogenetics to cultural anthropology" (No. 075-15-2019-1879) Kalmyk Scientific Center of the Russian Academy of Sciences, Elista, Russia 358000.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2021.102894.

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