Archaeological Research in Asia xxx (xxxx) xxxx

Contents lists available at ScienceDirect

Archaeological Research in Asia

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

Case report

Mitochondrial DNA of domesticated sheep confirms pastoralist component of Afanasievo subsistence economy in the Altai Mountains (3300–2900 cal BC)

Taylor R. Hermes[a,*], Alexey A. Tishkin[b], Pavel A. Kosintsev[c], Nadezhda F. Stepanova[d], Ben Krause-Kyora[e], Cheryl A. Makarewicz[a,*]

[a] Institute of Prehistoric and Protohistoric Archaeology, Kiel University, Johanna-Mestorf-Straße 2-6, 24118 Kiel, Germany
[b] Department of Archaeology, Ethnography and Museology, Altai State University, Prospekt Lenina, 61, Barnaul 656049, Russia
[c] Laboratory of Paleoecology, Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, Ulitsa 8 Marta, 202, Yekaterinburg 620144, Russia
[d] Institute of Archaeology and Ethnography, Siberian Branch, Russian Academy of Sciences, Prospekt Akademika Lavrent'eva, 17, Novosibirsk 630090, Russia
[e] Institute of Clinical Molecular Biology, Kiel University, University Hospital Schleswig-Holstein, Rosalind-Franklin-Straße 12, 24105 Kiel, Germany

ARTICLE INFO

Keywords:
Afanasievo culture
Nizhnyaya Sooru
Altai Republic
Eneolithic
Pastoralism

ABSTRACT

The initial spread of pastoralist subsistence to Inner Asia remains poorly defined due in part to limited research on settlement sites dating to the Eneolithic period (ca. 3600–2900 cal BC) in the Altai Mountains. The emergence of the Afanasievo culture in the Altai Mountains appears to have coincided with the arrival of domesticated sheep, goats, and cattle. However, Afanasievo sites also contain wild counterparts of these domesticated livestock species, which calls into question previous faunal identifications between analysts. We analyzed sequences of the mitochondrial cytochrome *b* gene of faunal skeletal remains from the Afanasievo settlement site Nizhnyaya Sooru to test for the presence of domesticated sheep (*Ovis aries*) and goats (*Capra hircus*). Five out of five analyzed tooth specimens were identified as *Ovis aries*, and radiocarbon determinations taken from two of these date to ca. 3300–2900 cal BC. This research provides an important chronological point of reference for the earliest spread of Near Eastern domesticated animals to Inner Asia.

1. Introduction

Archaeologists have long thought that the initial spread of domesticated sheep, goats, and cattle to Inner Asia coincided with the emergence of the Eneolithic Afanasievo culture in the Altai Mountains during the second half of the fourth millennium BCE (Gryaznov, 1999; Gryaznov and Vadetskaya, 1968; Kiselev, 1938; Pogozheva, 2006; Teploukhov, 1929; Tsyb, 1984). Similarity in ceramic forms and decorative styles, as well as mortuary practices that involved placing individuals in a crouched position in kurgan burials, used by Afanasievo communities and those located in the Circum-Pontic steppe supported narratives that migrations of so-called Yamnaya or Repin herders to the Altai gave rise to the Afanasievo culture (e.g., Anthony, 2007). More likely, however, Yamnaya and Afanasievo peoples shared a cultural source and subsequently developed similar material culture.

Human genomic research showing indistinguishable genetic variation between individuals recovered from Yamnaya and Afanasievo sites thus far suggests that long-distance movements across the vast steppe grasslands took place without in-coming people genetically admixing with communities characterized by “Ancient North Eurasian” ancestry along the way (Allentoft et al., 2015; Damgaard et al., 2018; Haak et al., 2015; Jeong et al., 2020; Mathieson et al., 2015; Narasimhan et al., 2019; Wang et al., 2020). Eneolithic herders moving from the western steppe into the Altai region may have passed the steppes of northern Kazakhstan and southwest Siberia that were occupied by communities managing domesticated Przewalski's horses (*Equus przewalskii*) (Fig. 1) (Gaunitz et al., 2018; Outram et al., 2009), but so far, no evidence suggests that exchanges of domesticates occurred.

Interestingly, both the scale of “western steppe” population movement into the Altai and depth of integration with diverse communities of local hunter-gatherers appear to have been rather limited during the Eneolithic period. So far, only faint signals of Yamnaya-related ancestry are detectable in subsequent populations of the Altai and proximal regions to the east (Damgaard et al., 2018; Jeong et al., 2020; Jeong et al., 2018; Narasimhan et al., 2019; Wang et al., 2020). In contrast, up to ca. 50% Yamnaya-related ancestry is present in individuals recovered from

* Corresponding authors.
E-mail addresses: trhermes@gmail.com (T.R. Hermes), c.makarewicz@ufg.uni-kiel.de (C.A. Makarewicz).

https://doi.org/10.1016/j.ara.2020.100232
Received 13 December 2019; Received in revised form 30 September 2020; Accepted 5 October 2020

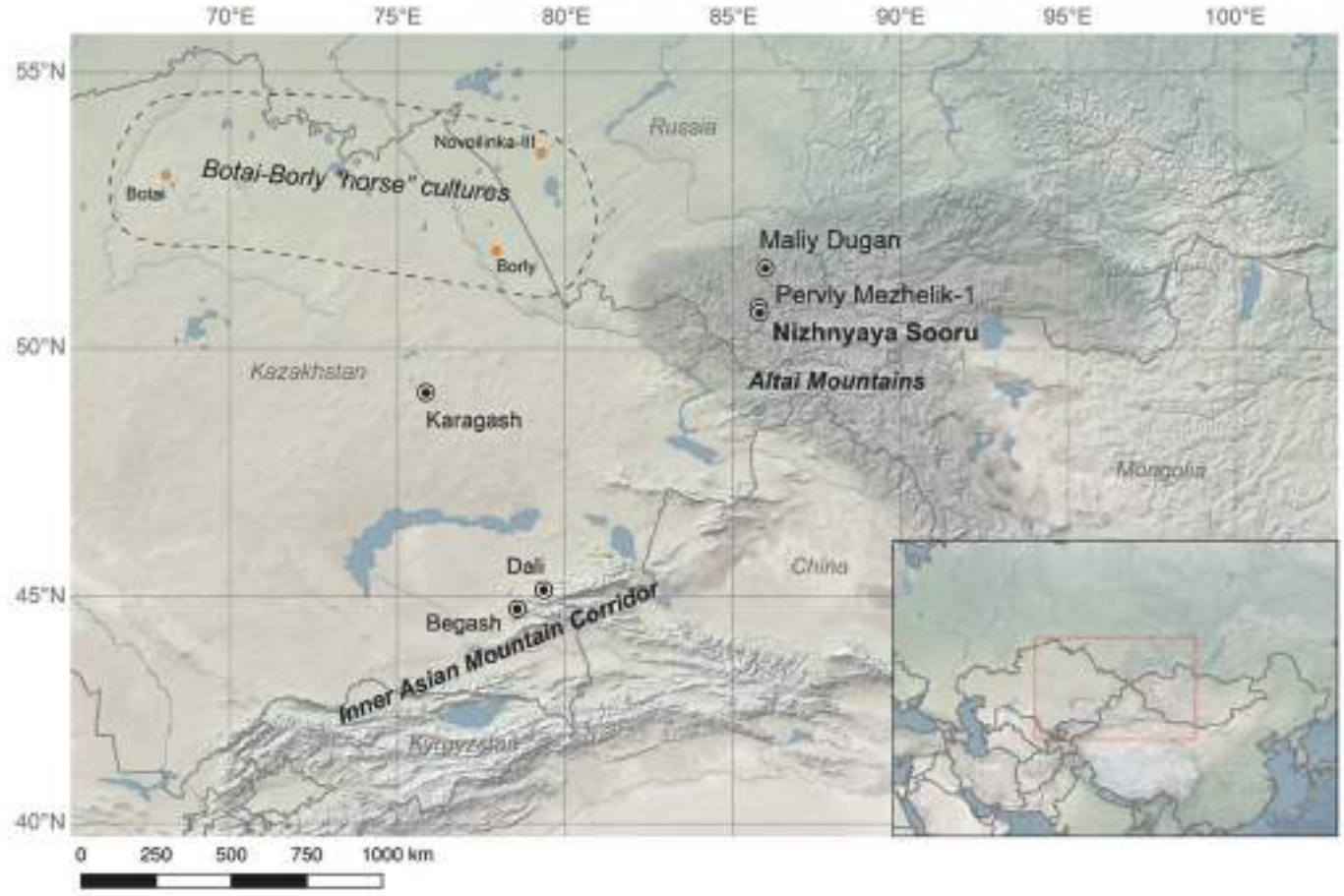

Fig. 1. Map of Inner Asia showing the location of Nizhnyaya Sooru relative to other sites providing radiocarbon dates for early domesticated sheep/goat remains listed in Table 2, in addition to key sites representing the Eneolithic Botai-Borly cultural sphere.

steppe regions adjacent to the Tian Shan and western Pamir Mountains dating to ca. 1700 cal BC and centuries later (Narasimhan et al., 2019; Ning et al., 2019). Afanasievo communities appear to have maintained strong intra-group exclusivity, when considering that Afanasievo cemeteries contain tight-knit kin groups of first, second, and third degree relatives (Narasimhan et al., 2019). Out of 36 Afanasievo individuals yielding genome-wide data, researchers have identified only four individuals prominently exhibiting Ancient North Eurasian ancestry with minor western steppe components that were buried according to Afanasievo traditions, which were dated to the early-late third millennium BC at the end of the Afanasievo cultural sequence (Damgaard et al., 2018; Jeong et al., 2020; Wang et al., 2020). Durable group cohesion by Afanasievo newcomers to the Altai and by subsequent generations corresponds to social mechanisms of migrants memorializing their distant homeland through high-fidelity replication of material culture (Trabert, 2019). Nonetheless, answering questions about the nature of Afanasievo animal exploitation strategies, including the use of domesticates remains impeded by limited research on Afanasievo settlements.

Previous zooarchaeological research at Afanasievo settlement and mortuary sites argues for the exploitation of both domesticated and wild cattle, sheep, and goats (Derevianko and Molodin, 1994; Gryaznov, 1999; Kosintsev, 2005; Kosintsev and Stepanova, 2010; Pogozheva, 2006). However, the biogeographic distribution of Siberian ibex (*Capra sibirica*) and argali sheep (*Ovis ammon*) includes the Altai (Baskin and Danell, 2003), while aurochsen (*Bos primigenius*) were also likely present in the region. Consequently, the relative importance of hunting and herding in Afanasievo communities remains ambiguous (Frachetti, 2012). Shared skeletal morphology between domesticated livestock bovids and their wild counterparts complicates establishing species representation, while high fragmentation of faunal skeletal remains recovered from Afanasievo sites further impedes biometrical analysis that can assist in assessing the use of domesticated animals (Shul'ga, 2012).

Here, we test for the presence of domesticated sheep (*Ovis aries*) and goat (*Capra hircus*) at the Afanasievo settlement Nizhnyaya Sooru located in the upper Karakol river in the Altai Republic, Russia (Fig. 1). Previous archaeological research at Nizhnyaya Sooru identified occupational layers containing Afanasievo ceramics and stone tools, in addition to abundant faunal skeletal remains (Larin et al., 1998). To provide concrete taxonomic identifications of both domesticated and wild sheep and goats, we employ ancient DNA analysis of the mitochondrial cytochrome *b* gene (*MT-CYB*), which codes for a protein used in cellular respiration that is highly conserved and useful for resolving taxonomic relationships (Irwin et al., 1991). Laboratory methods and analytical protocols followed Hermes et al. (2019). We also obtained radiocarbon determinations from faunal specimens providing *MT-CYB* sequences.

2. Previous research at Nizhnyaya Sooru

Excavations of Nizhnyaya Sooru were conducted in 1994 and opened 2.4 m^2 of the settlement area, revealing a 16-cm cultural layer approximately 60 cm below the modern surface that contained faunal skeletal remains, ceramics sherds, and lithics (Larin et al., 1998). Unlike the relatively few Afanasievo settlements discovered to date, Nizhnyaya Sooru does not contain later occupational layers and, thus, provides a pristine record of Afanasievo cultural deposits (Larin et al., 1998).

The material culture recovered at Nizhnyaya Sooru is linked to the

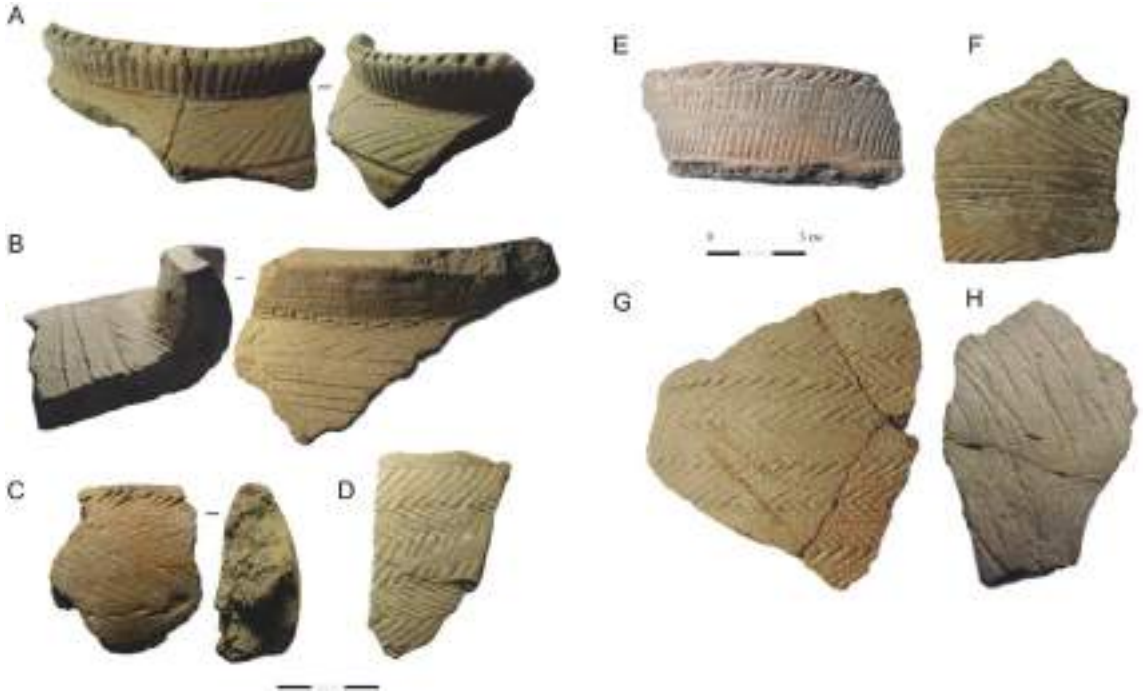

Fig. 2. Ceramic sherds recovered by Larin et al. (1998) from the Nizhnyaya Sooru settlement. (A-C) rims of vessels, including (B) a large spherical pot and (C) a small bowl with thick walls, thought to be used for incense burning. (D) Fragment of a base. (E-H) Sherds exhibiting rocker-stamp impressions that are common in Afanasievo ceramic assemblages. Rim decorations consisting of tear-drop incisions (B, C, and E) and highly regular rocking zigzags (E) are uncommon Afanasievo styles.

regional Afanasievo archaeological horizon, but Larin et al. (1998) note that ceramic decorations exhibit some stylistic departures from the canonical definition of the Afanasievo ceramic material assemblage (Fig. 2). This distinction is most visible in a decorative technique of tear-drop marks around the rims (Fig. 2 B, C, & E), including a rim with rocking stamp impressions, showing a regular zigzag pattern with sharp angles (Fig. 2 E). Vessels with unusual ornamental elements have also been observed at several other Afanasievo sites, including Perviy Mezhelik-1, Malinovyj Log, Karasuk-3, and Ust'-Kuyumskij (Stepanova, 2010). While the ceramics assemblage of Nizhnyaya Sooru is not unique in general terms, additional research is needed to assess bilateral cultural exchanges with local hunter-gatherer communities that produced pottery prior to the Afanasievo horizon (cf. Kiryushin and Kiryushin, 2005).

Previous zooarchaeological analysis of the faunal assemblage from Nizhnyaya Sooru concluded that domesticated herbivores were of primary importance (Kosintsev, 2005). Out of 476 recovered faunal specimens from Nizhnyaya Sooru, 278 were at the time identified to species (Table 1; Kosintsev, 2005). Caprines (*Ovis* or *Capra*) were the predominant taxon recovered at Nizhnyaya Sooru (n = 229), representing 82.3% of identified specimens. Moreover, 41 caprine specimens were recorded as likely belonging to *Ovis*. *Bos* spp., either domesticated *Bos taurus* or wild aurochs (*Bos primigenius*), were the second most abundant species representing 14.7% of identified specimens. Other large mammals in the assemblage are represented by horse (*Equus* sp.) and red deer (*Cervus* sp.), together accounting for ca. 2% of identified specimens. Small game includes one bone each from a fox (*Vulpes* sp.) and a badger (*Meles* sp.).

Table 1
Number of identified specimens (NISP), percent NISP, and minimum number of individuals (MNI) of faunal taxa recovered from Nizhnyaya Sooru after Kosintsev (2005). Taxonomic groups are reconfigured here to reflect genus-level identifications.

Taxon	NISP	%NISP	MNI
Bos spp.	41	14.7	5
Ovis/Capra spp.	229	82.3	19
Equus sp.	4	1.4	2
Cervus sp.	2	< 1	1
Vulpes sp.	1	< 1	1
Meles sp.	1	< 1	1
Total	278	100	29
Unidentifiable	198	–	–

3. Results

3.1. Genetic species identification

MT-CYB sequences (110-bp) were successfully recovered from five out of five tooth specimens with duplicates from two independent extractions. Three haplotypes were represented in the sample set, which are identical to known haplotypes of *Ovis aries* (Fig. 3). Notably, the recovery of a rare *MT-CYB* haplotype from sample KO182010 was surprising given a limited sample size. As mitochondrial DNA does not recombine, this haplotype has been shown to accompany D lineage haplotypes in hypervariable region 1 based on reference data. So far, only six individuals out of 1231 modern sheep previously analyzed from Eurasia belong to haplogroup D (Demirci et al., 2013; Meadows et al., 2011; Tapio et al., 2006). A recent paleogenetic study of sheep dating from the early Bronze Age to historical periods in the Altai region recovered one D haplotype out of 40 samples tested (Kechin et al., 2019). The *MT-CYB* sequence of sample KO182010 was identical to that of a domesticated sheep recovered from the early Bronze Age site of Dali (ca. 2700 cal BC) located in the Dzhungar Mountains of southeastern Kazakhstan (Fig. 3; Hermes et al., 2019).

3.2. Radiocarbon dating

AMS radiocarbon determinations were obtained from dentinal collagen of two samples providing domesticated sheep *MT-CYB* sequences,

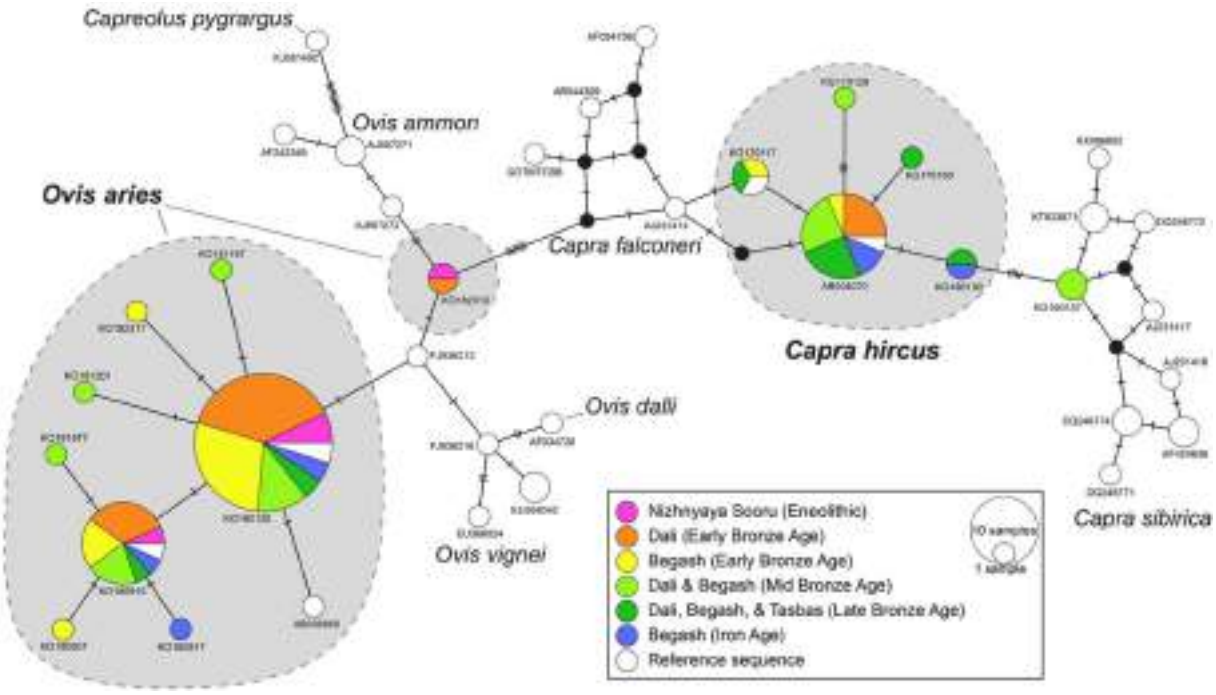

Fig. 3. Median joining network of *MT-CYB* sequences recovered from Nizhnyaya Sooru in comparison to *MT-CYB* sequences recovered by Hermes et al. (2019) from multi-period sites of Dali, Begash, and Tasbas located in the central Inner Asian Mountain Corridor of southeastern Kazakhstan. Reference *MT-CYB* sequences of *Ovis aries* and *Capra hircus* and wild *Ovis* and *Capra* spp. and *Capreolus pygargus* help visualize the genetic diversity observed between species. The network was produced using PopART v. 1.7.2 (Bandelt et al., 1999; Leigh and Bryant, 2015).

Table 2
AMS ^{14}C dates of domesticated sheep from Nizhnyaya Sooru and faunal specimens from the Afanasievo settlement Malyi Dugan and human burial #12 from Perviy Mezhelik-1 (Altai Republic, Russia). Also included are AMS ^{14}C dates from specimens providing a *MT-CYB* sequence of *Ovis aries* from the early Bronze Age sites Dali and Begash located in the Dzhungar Mountains (Kazakhstan), in addition to an AMS ^{14}C date from a human buried with purported domesticated caprine remains at Karagash located in central Kazakhstan. [1]Data from Svyatko et al. (2017a). [2]Data from Hermes et al. (2019). [3]Data from Motuzaite Matuzeviciute et al. (2015).

							Calibrated BC (2σ)		
Site	aDNA ID	^{14}C ID	Taxon	Material	^{14}C years (BP)	±	From	To	Mean
Nizhnyaya Sooru	KO182009	Poz-113280	*Ovis aries*	Dentine	4460	40	3346	2945	3173
Nizhnyaya Sooru	KO182013	Poz-113281	*Ovis aries*	Dentine	4320	40	3081	2883	2952
Malyi Dugan[1]	–	UBA-22989	Ovicaprid	Collagen	4209	34	2901	2677	2796
Malyi Dugan[1]	–	UBA-22990	*Capreolus*	Collagen	4197	36	2896	2666	2782
Perviy Mezhelik-1[1]	–	UBA-29309	Ovicaprid/*Capreolus*	Collagen	4473	35	3341	3026	3197
Dali[2]	KO180909	Beta-484122	*Ovis aries*	Dentine	4080	30	2855	2495	2645
Begash[2]	KO180907	Poz-88835	*Ovis aries*	Collagen	3830	30	2460	2150	2285
Karagash[3]	–	UBA-22949	Human	Collagen	4257	32	2920	2759	2876

following established protocols at the Poznan Radiocarbon Laboratory (Piotrowska and Goslar, 2002). Raw ^{14}C ages were calibrated using the IntCal13 curve in OxCal v4.3.2 (Bronk Ramsey, 2017; Reimer et al., 2013). The two obtained dates overlap and collectively range from ca. 3350 to 2900 cal BC (Table 2). The older determination calibrates to a wide interval of 3346–2945 cal BC (KO182009), in part due to a 250-year period of shifting directionality set within a plateau in the radiocarbon calibration curve (Fig. 4). The younger determination dating to 3081–2883 cal BC (KO182013) provides a relatively narrow calibrated range, despite falling on the end of a 75-year plateau (Fig. 4).

4. Discussion

Domesticated sheep at Nizhnyaya Sooru directly dated to the late fourth and early third millennia BCE represent the earliest known food producing technology in Inner Asia that had its origins in the Near East. Prior to this study, only three radiocarbon dates were obtained from faunal remains recovered from the Afanasievo settlement Malyi Dugan and cemetery Perviy Mezhelik-1; two of these specimens were ambiguously identified to *Ovis/Capra* or *Ovis/Capra/Capreolus*, while the third was identified as *Capreolus* (Svyatko et al., 2017a, 2017b). These Eneolithic dates are broadly contemporaneous with the new dates from Nizhnyaya Sooru (Table 2), which coincide with a revised "core" chronology for the Afanasievo cultural horizon in the Altai ranging between ca. 3100 to 2900 cal BC (cf. Poliakov et al., 2019).

Human remains in direct association with faunal skeletal remains identified as *Ovis/Capra* in an Afanasievo-style burial at the site of Karagash located in central Kazakhstan were directly dated to 2920–2712 cal BC (Table 2; Motuzaite Matuzeviciute et al., 2015). A critical issue with radiocarbon determinations measured from human bone collagen in regions where aquatic resources were available is the reservoir effect causing dates to appear older, which may be an issue in central Eurasia due to ancient fish consumption (Svyatko et al., 2017b; Svyatko et al., 2015). Analysts have long suspected that ancient steppe pastoralists consumed fish, based on high nitrogen isotopic values of bulk human bone collagen (Lightfoot et al., 2015; Murphy et al., 2013;

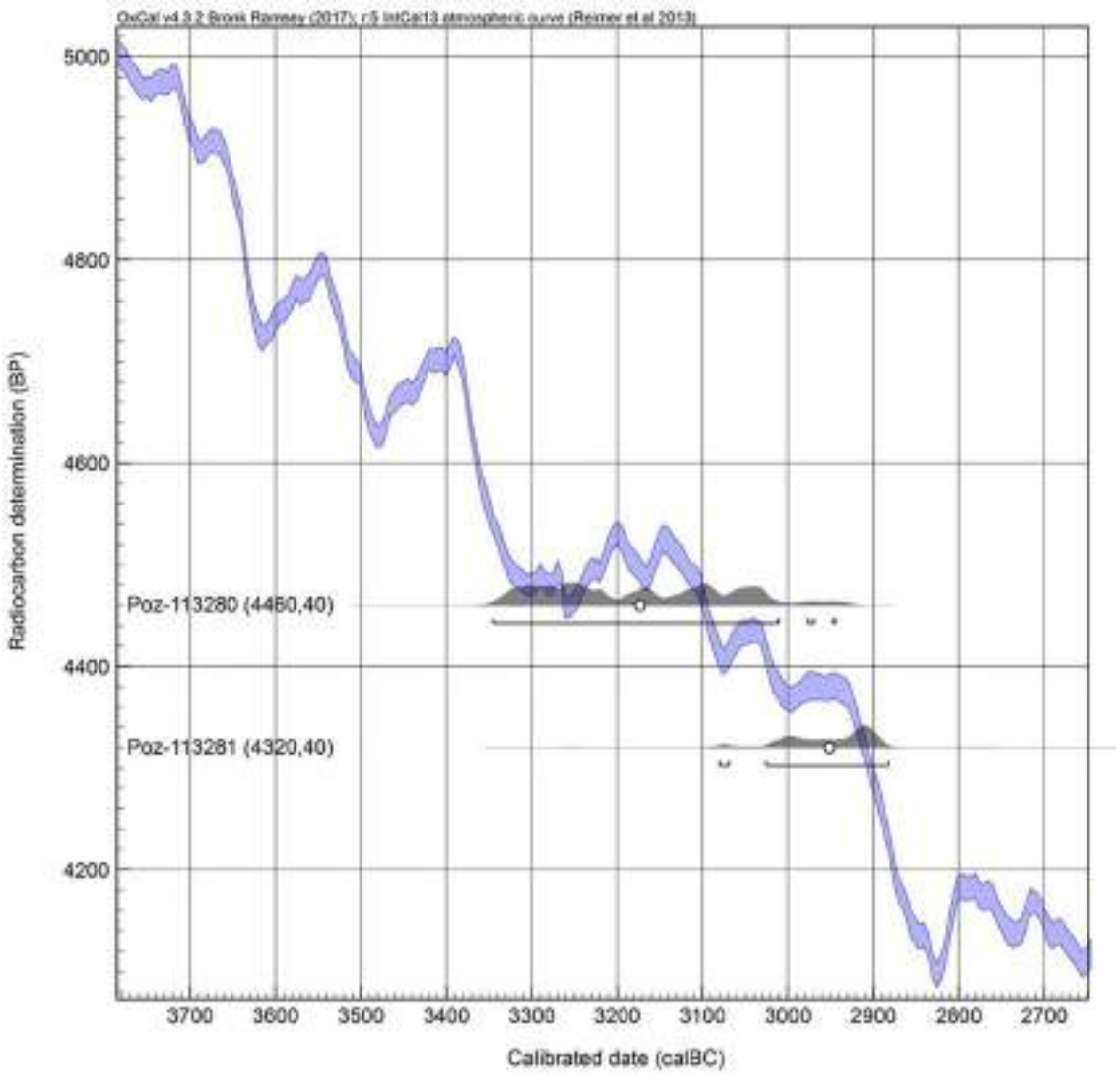

Fig. 4. Calibrated radiocarbon determinations of domesticated sheep recovered from Nizhnyaya Sooru are shown superimposed on the IntCal13 curve (blue).

O'Connell, 2003; Privat et al., 2007; Svyatko et al., 2013; Ventresca Miller et al., 2014). Notwithstanding, a vast majority of radiocarbon dates from Afanasievo sites were measured on human bone collagen or unidentified charcoals recovered from burial tumuli (Damgaard et al., 2018; Narasimhan et al., 2019; Poliakov et al., 2019; Taylor et al., 2019; Wilkin et al., 2020), the latter of which may give inbuilt ages due to the "old wood effect" (Schiffer, 1986). Therefore, our radiocarbon determinations from specimens confirmed to be *Ovis aries* with *MT-CYB* sequences provide a robust chronological marker in Inner Asia for the earliest so far identified pastoralist livestock that were domesticated in the Near East.

It is probable that herders moving from the western steppes to the Altai region were managing sheep, goats, and cattle together. Domesticated sheep may have reached the Altai as western steppe herders passed through steppe regions in northern Kazakhstan. There, Przewalski's horses were indigenously domesticated by communities of the Botai-Borly cultural sphere by 3600–3100 cal BC (Gaunitz et al., 2018; Outram et al., 2009), which likely extended into southwestern Siberia where the contemporaneous Novoilinka-III settlement further echoes a narrowly focused, horse-based subsistence economy (Fig. 1) (Kiryushin, 2015; Kuslij et al., 2019; Vasil'ev et al., 2011). So far, there remains a lack of evidence for cultural contact between Afanasievo forerunners and Botai-Borly communities (cf. Anthony, 2007).

5. Future directions

Overall, more research is needed on stratified settlements containing Afanasievo cultural material. Series of new radiocarbon dates from collagen of well-identified terrestrial faunal remains sourced from secure occupational strata would 1) inform Bayesian radiocarbon chronologies to work through the plateau in the radiocarbon calibration curve between 3325 and 2900 cal BC, and 2) circumvent aging effects that have so far hampered chronologies of the Afanasievo horizon (cf. Poliakov et al., 2019). To date, only a handful of settlement sites yielding Afanasievo materials have been radiocarbon dated, which after Nizhnyaya Sooru include, Kara-Tenesh, Malyi Dugan, Kaminnaya Cave, and Denisova Cave (Derevianko and Molodin, 1994; Orlova, 1995; Svyatko et al., 2017a). While these dating efforts provided an initial chronological scaffolding for the Eneolithic, most of these dates were obtained using older instrumentation that generated wide analytical errors. Improved chronological resolution of Afanasievo occupations would bolster further zooarchaeological analyses in order to illuminate precise pastoralist strategies in effect at Afanasievo sites and possible subsistence shifts through time. Along these lines, additional analysis of material culture from Afanasievo and local hunter-gathering communities in the Altai may reveal cultural dynamics that are poorly reflected in human paleogenetic data.

The recovery of a rare *MT-CYB* haplotype of domesticated sheep

that is diagnostic of haplogroup D at Nizhnyaya Sooru, which was also recovered from layers dating to the mid-third millennium BCE at Dali, does not yet resolve the earliest transmission of pastoralist livestock to Inner Asia. In strict chronological terms, these data would suggest that pastoralism spread into the Altai Mountains and then southward into the central Inner Asian Mountain Corridor (IAMC). Previous paleogenetic work on domesticated sheep from archaeological sites in the Altai region postdating the Afanasievo period show that the region was characterized by diverse mitochondrial haplotypes (Dymova et al., 2019; Dymova et al., 2017; Kechin et al., 2019). Additional paleogenetic research spanning whole genomes of directly radiocarbon dated specimens is needed to test whether this scenario, a northward transmission of domesticated ruminants via the IAMC, or a complex combination of both contributed to the spread of pastoralism into Inner Asia and farther east into Mongolia and China.

Data availability

Genetic sequences recovered in this study have been deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank), accession nos. MN794054-MN794058.

Declaration of Competing Interest

None.

Acknowledgements

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no. 772957/ASIAPAST held by C.A. Makarewicz). This research was also supported by the Russian Science Foundation, project no. 16-18-10033 "Formation and Evolution of the Subsistence System of the Nomadic Societies of Altai and Adjacent Territories in Late Antiquity and the Middle Ages: Complex Reconstruction" held by A.A. Tishkin.

References

Allentoft, M.E., Sikora, M., Sjögren, K.-G., Rasmussen, S., Rasmussen, M., Stenderup, J., Damgaard, P.B., Schroeder, H., Ahlström, T., Vinner, L., Malaspinas, A.-S., Margaryan, A., Higham, T., Chivall, D., Lynnerup, N., Harvig, L., Baron, J., Casa, P.D., Dąbrowski, P., Duffy, P.R., Ebel, A.V., Epimakhov, A., Frei, K., Furmanek, M., Gralak, T., Gromov, A., Gronkiewicz, S., Grupe, G., Hajdu, T., Jarysz, R., Khartanovich, V., Khokhlov, A., Kiss, V., Kolář, J., Kriiska, A., Lasak, I., Longhi, C., McGlynn, G., Merkevicius, A., Merkyte, I., Metspalu, M., Mkrtchyan, R., Moiseyev, V., Paja, L., Pálfi, G., Pokutta, D., Pospieszny, Ł., Price, T.D., Saag, L., Sablin, M., Shishlina, N., Smrčka, V., Soenov, V.I., Szeverényi, V., Tóth, G., Trifanova, S.V., Varul, L., Vicze, M., Yepiskoposyan, L., Zhitenev, V., Orlando, L., Sicheritz-Pontén, T., Brunak, S., Nielsen, R., Kristiansen, K., Willerslev, E., 2015. Population genomics of Bronze Age Eurasia. Nature 522, 167–172. https://doi.org/10.1038/nature14507.

Anthony, D., 2007. The Horse, the Wheel, and Language: How Bronze-Age Riders from the Eurasian Steppes Shaped the Modern World. Princeton University Press, Princeton.

Bandelt, H.J., Forster, P., Röhl, A., 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. 16, 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036.

Baskin, L., Danell, K., 2003. Ecology of Ungulates: A Handbook of Species in Eastern Europe and Northern and Central Asia. Springer-Verlag, Berlin.

Bronk Ramsey, C., 2017. Methods for summarizing radiocarbon datasets. Radiocarbon 59, 1809–1833. https://doi.org/10.1017/RDC.2017.108.

Damgaard, P. de B., Martiniano, R., Kamm, J., Moreno-Mayar, J.V., Kroonen, G., Peyrot, M., Barjamovic, G., Rasmussen, S., Zacho, C., Baimukhanov, N., Zaibert, V., Merz, V., Biddanda, A., Merz, I., Loman, V., Evdokimov, V., Usmanova, E., Hemphill, B., Seguin-Orlando, A., Yediay, F.E., Ullah, I., Sjögren, K.-G., Iversen, K.H., Choin, J., de la Fuente, C., Ilardo, M., Schroeder, H., Moiseyev, V., Gromov, A., Polyakov, A., Omura, S., Senyurt, S.Y., Ahmad, H., McKenzie, C., Margaryan, A., Hameed, A., Samad, A., Gul, N., Khokhar, M.H., Goriunova, O.I., Bazaliiskii, V.I., Novembre, J., Weber, A.W., Orlando, L., Allentoft, M.E., Nielsen, R., Kristiansen, K., Sikora, M., Outram, A.K., Durbin, R., Willerslev, E., 2018. The first horse herders and the impact of early Bronze Age steppe expansions into Asia. Science eaar7711. https://doi.org/10.1126/science.aar7711.

Demirci, S., Koban Baştanlar, E., Dağtaş, N.D., Pişkin, E., Engin, A., Özer, F., Yüncü, E., Doğan, Ş.A., Togan, İ., 2013. Mitochondrial DNA diversity of modern, ancient and wild sheep (*Ovis gmelinii anatolica*) from Turkey: new insights on the evolutionary history of sheep. PLoS ONE 8, e81952. https://doi.org/10.1371/journal.pone.0081952.

Derevianko, A.P., Molodin, V.I., 1994. Denisova Peshchera. Nauka, Novosibirsk.

Dymova, M.A., Zadorozhny, A.V., Mishukova, O.V., Khrapov, E.A., Druzhkova, Trifonov, V.A., Kichigin, I.G., Tishkin, A.A., Grushin, S.P., Filipenko, M.L., 2017. Mitochondrial DNA analysis of ancient sheep from Altai. Anim. Genet. 48, 615–618. https://doi.org/10.1111/age.12569.

Dymova, M.A., Tishkin, A.A., Mishukova, O.V., Khrapov, E.A., Grushin, S.P., Filipenko, M.L., 2019. Gaplotipicheskoe raznoobraziye domashnej ovtsy (*Ovis aries*) (po materialam arkheologicheskikh pamyatnikov pannej bronzy yuga zapadnoj Sibiri). Zool. Zhurnal 98, 836–842. https://doi.org/10.1134/S0044513419070043.

Frachetti, M.D., 2012. Multiregional emergence of mobile pastoralism and nonuniform institutional complexity across Eurasia. Curr. Anthropol. 53, 2–38. https://doi.org/10.1086/663692.

Gaunitz, C., Fages, A., Hanghøj, K., Albrechtsen, A., Khan, N., Schubert, M., Seguin-Orlando, A., Owens, I.J., Felkel, S., Bignon-Lau, O., Damgaard, P. de B., Mittnik, A., Mohaseb, A.F., Davoudi, H., Alquraishi, S., Alfarhan, A.H., Al-Rasheid, K.A.S., Crubézy, E., Benecke, N., Olsen, S., Brown, D., Anthony, D., Massy, K., Pitulko, V., Kasparov, A., Brem, G., Hofreiter, M., Mukhtarova, G., Baimukhanov, N., Lõugas, L., Onar, V., Stockhammer, P.W., Krause, J., Boldgiv, B., Undrakhbold, S., Erdenebaatar, D., Lepetz, S., Mashkour, M., Ludwig, A., Wallner, B., Merz, V., Merz, I., Zaibert, V., Willerslev, E., Librado, P., Outram, A.K., Orlando, L., 2018. Ancient genomes revisit the ancestry of domestic and Przewalski's horses. Science 360, 111–114. https://doi.org/10.1126/science.aao3297.

Gryaznov, M.P., 1999. Afanas'evskaya Kul'tura na Yenesee. Izd-vo "Dmitriy Bulanin," Saint Petersburg.

Gryaznov, M.P., Vadetskaya, E.B., 1968. Afanasievskaya kul'tura, in: Istoriya Sibiri. Leningrad. pp. 159–165.

Haak, W., Lazaridis, I., Patterson, N., Rohland, N., Mallick, S., Llamas, B., Brandt, G., Nordenfelt, S., Harney, E., Stewardson, K., Fu, Q., Mittnik, A., Bánffy, E., Economou, C., Francken, M., Friederich, S., Pena, R.G., Hallgren, F., Khartanovich, V., Khokhlov, A., Kunst, M., Kuznetsov, P., Meller, H., Mochalov, O., Moiseyev, V., Nicklisch, N., Pichler, S.L., Risch, R., Guerra, M.A.R., Roth, C., Szécsényi-Nagy, A., Wahl, J., Meyer, M., Krause, J., Brown, D., Anthony, D., Cooper, A., Alt, K.W., Reich, D., 2015. Massive migration from the steppe was a source for Indo-European languages in Europe. Nature 522, 207. https://doi.org/10.1038/nature14317.

Hermes, T.R., Frachetti, M.D., Doumani Dupuy, P.N., Mar'yashev, A., Nebel, A., Makarewicz, C.A., 2019. Early integration of pastoralism and millet cultivation in Bronze Age Eurasia. Proc. R. Soc. B 286, 20191273. https://doi.org/10.1098/rspb.2019.1273.

Irwin, D.M., Kocher, T.D., Wilson, A.C., 1991. Evolution of the cytochrome *b* gene of mammals. J. Mol. Evol. 32, 128–144. https://doi.org/10.1007/BF02515385.

Jeong, C., Wilkin, S., Amgalantugs, T., Bouwman, A.S., Taylor, W.T.T., Hagan, R.W., Bromage, S., Tsolmon, S., Trachsel, C., Grossmann, J., Littleton, J., Makarewicz, C.A., Krigbaum, J., Burri, M., Scott, A., Davaasambuu, G., Wright, J., Irmer, F., Myagmar, E., Boivin, N., Robbeets, M., Rühli, F.J., Krause, J., Frohlich, B., Hendy, J., Warinner, C., 2018. Bronze Age population dynamics and the rise of dairy pastoralism on the eastern Eurasian steppe. Proc. Natl. Acad. Sci. 115, E11248–E11255. https://doi.org/10.1073/pnas.1813608115.

Jeong, C., Wang, K., Wilkin, S., Taylor, W.T.T., Miller, B.K., Ulziibayar, S., Stahl, R., Chiovelli, C., Bemmann, J.H., Knolle, F., Kradin, N., Bazarov, B.A., Miyagashev, D.A., Konovalov, P.B., Zhambaltarova, E., Miller, A.V., Haak, W., Schiffels, S., Krause, J., Boivin, N., Myagmar, E., Hendy, J., Warinner, C., 2020. A dynamic 6,000-year genetic history of Eurasia's Eastern Steppe. bioRxiv. https://doi.org/10.1101/2020.03.25.008078. 2020.03.25.008078.

Kechin, A.A., Dymova, M.A., Tishkin, A.A., Grushin, S.P., Dashkovskiy, P.K., Filipenko, M.L., 2019. Targeted sequencing for studying economically useful traits and phylogenetic diversity of ancient sheep. Russ. J. Genet. 55, 1499–1505. https://doi.org/10.1134/S102279541912007X.

Kiryushin, K.Yu, 2015. Morphology and decoration of ceramics from Novoilyinka III – a chalcolithic settlement in northern Kulunda, Southwestern Siberia. Archaeol. Ethnol. Anthropol. Eurasia 43, 28–39. https://doi.org/10.1016/j.aeae.2015.07.004.

Kiryushin, Yu.F., Kiryushin, K.Yu, 2005. K voprosu o roli neoliticheskogo komponenta v slozhenii afanas'evskoi kul'tury gornogo altaya. In: Korol', G.G. (Ed.), Arkheologiya Yuzhnoi Sibiri: Idei, Metody, Itkrytiya. Krasnoyarsk gosudarstvennyi pedagogicheskii universitet, Krasnoyarsk, pp. 26–28.

Kiselev, S.V., 1938. Sovetskaya arkheologiya Sibiri perioda metalla. Vestn. Drevnej Istor. 1, 228–243.

Kosintsev, P.A., 2005. Fauna poseleniya Nizhnyaya Sooru. In: Larin, O.V. (Ed.), Afanas'evskaya Kul'tura Gornogo Altaya: Mogilnik Sal'dyar-1. Izd-vo Alt. un-ta, Barnaul, pp. 160–167.

Kosintsev, P.A., Stepanova, N.F., 2010. Fauna Afanas'evskogo poseleniya Malyi Dugan. In: Stepanova, N.F., Polyakov, A.V. (Eds.), Afanas'evskii Sbornik: Sbornik Naushnykh Statei. Azbuka, Barnaul, pp. 121–129.

Kuslij, M.A., Kiryushin, K.Yu., Tishkin, A.A., Orlando, L., 2019. Molekulyarno-genetichеskij analiz kostnykh obraztsov drevnikh loshadej iz pamyatnika Botajskogo kruga Novoil'inka-III (Kulundinskaya step'). In: Materialy Mezhdunarodnoj Nauchno-Prakticheskoj Konferentsii "Botajskaya Kul'tura i Drugiye Eneoliticheskiye Pamyatniki Tsentral'noj Azii". KazNU imeni al'-Farabi, Almaty, pp. 64–65.

Larin, O.V., Kungurova, N.Yu., Stepanova, N.F., 1998. Poseleniye afanas'evskoj kul'tury Nizhnyaya Sooru. In: Kiryushin, Yu.F., Shamshin, A.B. (Eds.), Sokhraneniye i Izucheniye Kul'turnogo Naslediya Altajskogo Kraya. Barnaul, pp. 67–72.

Leigh, J.W., Bryant, D., 2015. Popart: full-feature software for haplotype network construction. Methods Ecol. Evol. 6, 1110–1116. https://doi.org/10.1111/2041-210X.

12410.
Lightfoot, E., Motuzaite-Matuzeviciute, G., O'Connell, T.C., Kukushkin, I.A., Loman, V., Varfolomeev, V., Liu, X., Jones, M.K., 2015. How 'pastoral' is pastoralism? Dietary diversity in Bronze Age communities in the Central Kazakhstan steppes. Archaeometry 57, 232–249. https://doi.org/10.1111/arcm.12123.
Mathieson, I., Lazaridis, I., Rohland, N., Mallick, S., Patterson, N., Roodenberg, S.A., Harney, E., Stewardson, K., Fernandes, D., Novak, M., Sirak, K., Gamba, C., Jones, E.R., Llamas, B., Dryomov, S., Pickrell, J., Arsuaga, J.L., de Castro, J.M.B., Carbonell, E., Gerritsen, F., Khokhlov, A., Kuznetsov, P., Lozano, M., Meller, H., Mochalov, O., Moiseyev, V., Guerra, M.A.R., Roodenberg, J., Vergès, J.M., Krause, J., Cooper, A., Alt, K.W., Brown, D., Anthony, D., Lalueza-Fox, C., Haak, W., Pinhasi, R., Reich, D., 2015. Genome-wide patterns of selection in 230 ancient Eurasians. Nature 528, 499–503. https://doi.org/10.1038/nature16152.
Meadows, J.R.S., Hiendleder, S., Kijas, J.W., 2011. Haplogroup relationships between domestic and wild sheep resolved using a mitogenome panel. Heredity 106, 700–706. https://doi.org/10.1038/hdy.2010.122.
Motuzaite Matuzeviciute, G., Lightfoot, E., O'Connell, T.C., Voyakin, D., Liu, X., Loman, V., Svyatko, S., Usmanova, E., Jones, M.K., 2015. The extent of cereal cultivation among the Bronze Age to Turkic period societies of Kazakhstan determined using stable isotope analysis of bone collagen. J. Archaeol. Sci. 59, 23–34. https://doi.org/10.1016/j.jas.2015.03.029.
Murphy, E.M., Schulting, R., Beer, N., Chistov, Y., Kasparov, A., Pshenitsyna, M., 2013. Iron Age pastoral nomadism and agriculture in the eastern Eurasian steppe: implications from dental palaeopathology and stable carbon and nitrogen isotopes. J. Archaeol. Sci. 40, 2547–2560. https://doi.org/10.1016/j.jas.2012.09.038.
Narasimhan, V.M., Patterson, N., Moorjani, P., Rohland, N., Bernardos, R., Mallick, S., Lazaridis, I., Nakatsuka, N., Olalde, I., Lipson, M., Kim, A.M., Olivieri, L.M., Coppa, A., Vidale, M., Mallory, J., Moiseyev, V., Kitov, E., Monge, J., Adamski, N., Alex, N., Broomandkhoshbacht, N., Candilio, F., Callan, K., Cheronet, O., Culleton, B.J., Ferry, M., Fernandes, D., Freilich, S., Gamarra, B., Gaudio, D., Hajdinjak, M., Harney, É., Harper, T.K., Keating, D., Lawson, A.M., Mah, M., Mandl, K., Michel, M., Novak, M., Oppenheimer, J., Rai, N., Sirak, K., Slon, V., Stewardson, K., Zalzala, F., Zhang, Z., Akhatov, G., Bagashev, A.N., Bagnera, A., Baitanayev, B., Bendezu-Sarmiento, J., Bissembaev, A.A., Bonora, G.L., Chargynov, T.T., Chikisheva, T., Dashkovskiy, P.K., Derevianko, A., Dobeš, M., Douka, K., Dubova, N., Duisengali, M.N., Enshin, D., Epimakhov, A., Fribus, A.V., Fuller, D., Goryachev, A., Gromov, A., Grushin, S.P., Hanks, B., Judd, M., Kazizov, E., Khokhlov, A., Krygin, A.P., Kupriyanova, E., Kuznetsov, P., Luiselli, D., Maksudov, F., Mamedov, A.M., Mamirov, T.B., Meiklejohn, C., Merrett, D.C., Micheli, R., Mochalov, O., Mustafokulov, S., Nayak, A., Pettener, D., Potts, R., Razhev, D., Rykun, M., Sarno, S., Savenkova, T.M., Sikhymbaeva, K., Slepchenko, S.M., Soltobaev, O.A., Stepanova, N., Svyatko, S., Tabaldiev, K., Teschler-Nicola, M., Tishkin, A.A., Tkachev, V.V., Vasilyev, S., Velemínský, P., Voyakin, D., Yermolayeva, A., Zahir, M., Zubkov, V.S., Zubova, A., Shinde, V.S., Lalueza-Fox, C., Meyer, M., Anthony, D., Boivin, N., Thangaraj, K., Kennett, D.J., Frachetti, M., Pinhasi, R., Reich, D., 2019. The formation of human populations in South and Central Asia. Science 365, eaat7487. https://doi.org/10.1126/science.aat7487.
Ning, C., Wang, C.-C., Gao, S., Yang, Y., Zhang, X., Wu, X., Zhang, F., Nie, Z., Tang, Y., Robbeets, M., Ma, J., Krause, J., Cui, Y., 2019. Ancient genomes reveal Yamnaya-related ancestry and a potential source of Indo-European speakers in Iron Age Tianshan. Curr. Biol. 29, 2526–2532.e4. https://doi.org/10.1016/j.cub.2019.06.044.
O'Connell, T.C., 2003. The importance of fish in the diet of central Eurasian peoples from the Mesolithic to the early Iron Age. In: Levine, M., Renfrew, C., Boyle, K. (Eds.), Prehistoric Steppe Adaptation and the Horse. McDonald Institute for Archaeological Research, Cambridge, pp. 253–268.
Orlova, L.A., 1995. Radiouglerodnoe datirovanie arkheologicheskikh pamyatnikov Sibiri i Dal'nego Vostoka. In: Metody Estestvennykh Nauk v Arkheologicheskikh Rekonstruktsiyakh. Novosibirsk, pp. 207–232.
Outram, A.K., Stear, N.A., Bendrey, R., Olsen, S., Kasparov, A., Zaibert, V., Thorpe, N., Evershed, R.P., 2009. The earliest horse harnessing and milking. Science 323, 1332–1335. https://doi.org/10.1126/science.1168594.
Piotrowska, N., Goslar, T., 2002. Preparation of bone samples in the Gliwice radiocarbon laboratory for AMS radiocarbon dating. Isot. Environ. Health Stud. 38, 267–275. https://doi.org/10.1080/10256010208033272.
Pogozheva, A.P., 2006. Afanas'evskaya Kul'tura. In: Pogozheva, A.P., Rykun, M.P., Stepanova, N.F., Tup, S.S. (Eds.), Epokha Eneolita i Bronzy Gornogo Altaya: Chast' 1. Azbuka, Barnaul, pp. 18–48.
Poliakov, A.V., Svyatko, S.V., Stepanova, N.F., 2019. A review of the radiocarbon dates for the Afanasyevo culture (Central Asia): shifting towards the "shorter" chronology. Radiocarbon 61, 243–263. https://doi.org/10.1017/RDC.2018.70.
Privat, K.L., O'Connell, T.C., Hedges, R.E.M., 2007. The distinction between freshwater- and terrestrial-based diets: methodological concerns and archaeological applications of sulphur stable isotope analysis. J. Archaeol. Sci. 34, 1197–1204. https://doi.org/10.1016/j.jas.2006.10.008.
Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A, Turney, C.S.M., 2013. INTCAL13 and MARINE13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55, 1869–1887.
Schiffer, M.B., 1986. Radiocarbon dating and the "old wood" problem: the case of the Hohokam chronology. J. Archaeol. Sci. 13, 13–30. https://doi.org/10.1016/0305-4403(86)90024-5.
Shul'ga, P.I., 2012. O khozyajstvye Afanas'evtsev gornogo Altaya. In: Stepanova, N.F. (Ed.), Afanas'evskij Sbornik 2: Sbornik Nuchnykh Statej. Azbuka, Barnaul, pp. 204–209.
Stepanova, N.F., 2010. Afanas'evskaya kul'tura gornogo Altaya i Yeniseya: pogrebal'nyj obryad i keramika (skhodstvo i raslichiye). In: Stepanova, N.F., Polyakov, A.V. (Eds.), Afanas'evskii Sbornik: Sbornik Naushnykh Statei. Azbuka, Barnaul, pp. 117–187.
Svyatko, S.V., Schulting, R.J., Mallory, J., Murphy, E.M., Reimer, P.J., Khartanovich, V.I., Chistov, Y.K., Sablin, M.V., 2013. Stable isotope dietary analysis of prehistoric populations from the Minusinsk Basin, southern Siberia, Russia: a new chronological framework for the introduction of millet to the eastern Eurasian steppe. J. Archaeol. Sci. 40, 3936–3945. https://doi.org/10.1016/j.jas.2013.05.005.
Svyatko, S.V., Mertz, I.V., Reimer, P.J., 2015. Freshwater reservoir effect on Redating of Eurasian steppe cultures: first results for Eneolithic and early Bronze Age Northeast Kazakhstan. Radiocarbon 57, 625–644. https://doi.org/10.2458/azu_rc.57.18431.
Svyatko, S.V., Polyakov, A.V., Soenov, V.I., Stepanova, N.F., Reimer, P.J., Ogle, N., Tyurina, E.A., Grushin, S.P., Rykun, M.P., 2017a. Stable isotope palaeodietary analysis of the early Bronze Age Afanasyevo culture in the Altai Mountains, southern Siberia. J. Archaeol. Sci. Rep. 14, 65–75. https://doi.org/10.1016/j.jasrep.2017.05.023.
Svyatko, S.V., Reimer, P.J., Schulting, R., 2017b. Modern freshwater reservoir offsets in the Eurasian steppe: implications for archaeology. Radiocarbon 1–11. https://doi.org/10.1017/RDC.2017.11.
Tapio, M., Marzanov, N., Ozerov, M., Ćinkulov, M., Gonzarenko, G., Kiselyova, T., Murawski, M., Viinalass, H., Kantanen, J., 2006. Sheep mitochondrial DNA variation in European, Caucasian, and central Asian areas. Mol. Biol. Evol. 23, 1776–1783. https://doi.org/10.1093/molbev/msl043.
Taylor, W., Wilkin, S., Wright, J., Dee, M., Erdene, M., Clark, J., Tuvshinjargal, T., Bayarsaikhan, J., Fitzhugh, W., Boivin, N., 2019. Radiocarbon dating and cultural dynamics across Mongolia's early pastoral transition. PLOS ONE 14, e0224241. https://doi.org/10.1371/journal.pone.0224241.
Teploukhov, S.A., 1929. Opyt klassifikatsii metallicheskikh kul'tur Minusinskogo kraya (v kratkom izlozhenii). In: Materialy Po Etnografii. 4. Nauka, Leningrad, pp. 41–62.
Trabert, S., 2019. Understanding the significance of migrants' material culture. J. Soc. Archaeol. 20, 95–115. https://doi.org/10.1177/1469605319879253.
Tsyb, S.V., 1984. Afanasevskaya kultura. In: Candidate of Science (History) Dissertation, Kemerovo.
Vasil'ev, S.A., Kiryushin, K.Yu., Sitinkov, S.M., Semibratov, V.P., 2011. Faunisticheskie ostatki iz poseleniya Novoil'inka-3 (po materialam paskopok 2010 goda). In: Problemy Arkheologii, Etnografii, Anthropologii Sibiri i Sopredelnykh Territorij. Izd-vo IAEt SO RAN, Novosibirsk, pp. 147–151.
Ventresca Miller, A., Usmanova, E., Logvin, V., Kalieva, S., Shevnina, I., Logvin, A., Kolbina, A., Suslov, A., Privat, K., Haas, K., Rosenmeier, M., 2014. Subsistence and social change in Central Eurasia: stable isotope analysis of populations spanning the Bronze Age transition. J. Archaeol. Sci. 42, 525–538. https://doi.org/10.1016/j.jas.2013.11.012.
Wang, C.-C., Yeh, H.-Y., Popov, A.N., Zhang, H.-Q., Matsumura, H., Sirak, K., Cheronet, O., Kovalev, A., Rohland, N., Kim, A.M., Bernardos, R., Tumen, D., Zhao, J., Liu, Y.-C., Liu, J.-Y., Mah, M., Mallick, S., Wang, K., Zhang, Z., Adamski, N., Broomandkhoshbacht, N., Callan, K., Culleton, B.J., Eccles, L., Lawson, A.M., Michel, M., Oppenheimer, J., Stewardson, K., Wen, S., Yan, S., Zalzala, F., Chuang, R., Huang, C.-J., Shiung, C.-C., Nikitin, Y.G., Tabarev, A.V., Tishkin, A.A., Lin, S., Sun, Z.-Y., Wu, X.-M., Yang, T.-L., Hu, X., Chen, L., Du, H., Bayarsaikhan, J., Mijiddorj, E., Erdenebaatar, D., Iderkhangai, T.-O., Myagmar, E., Kanzawa-Kiriyama, H., Nishino, M., Shinoda, K., Shubina, O.A., Guo, J., Deng, Q., Kang, L., Li, Dawei, Li, Dongna, Lin, R., Cai, W., Shrestha, R., Wang, L.-X., Wei, L., Xie, G., Yao, H., Zhang, M., He, G., Yang, X., Hu, R., Robbeets, M., Schiffels, S., Kennett, D.J., Jin, L., Li, H., Krause, J., Pinhasi, R., Reich, D., 2020. The genomic formation of human populations in East Asia. bioRxiv. https://doi.org/10.1101/2020.03.25.004606. 2020.03.25.004606.
Wilkin, S., Miller, A.V., Taylor, W.T.T., Miller, B.K., Hagan, R.W., Bleasdale, M., Scott, A., Gankhuyg, S., Ramsøe, A., Uliziibayar, S., Trachsel, C., Nanni, P., Grossmann, J., Orlando, L., Horton, M., Stockhammer, P.W., Myagmar, E., Boivin, N., Warinner, C., Hendy, J., 2020. Dairy pastoralism sustained eastern Eurasian steppe populations for 5,000 years. Nat. Ecol. Evol. 4, 346–355. https://doi.org/10.1038/s41559-020-1120-y.