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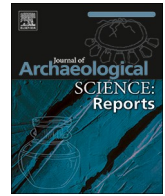
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Horse males became over-represented in archaeological assemblages during the Bronze Age

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ABSTRACT

The domestication of the horse and the development of new equestrian technologies have had a far-reaching impact on human history. Disentangling the respective role that horse males and females played during this process is, however, difficult based on iconography and osteological data alone. In this study, we leveraged an extensive ancient DNA time-series to determine the molecular sex of 268 horses spread across Eurasia and charted the male:female sex ratio through the last 40,000 years. We found even sex ratios in the Upper Palaeolithic and up until ~3900 years BP. However, we identified a striking over-representation of horse males in more recent osseous assemblages, which was particularly magnified in funerary contexts but also significant in non-ritual deposits. This suggests that the earliest horse herders managed males and females alike for more than one thousand years after domestication at Botai, but that the human representation and use of horses became gendered at the beginning of the Bronze Age, following the emergence of gender inequalities in human societies.

1. Introduction

The domestication of the horse some ~5500 years ago (Outram et al., 2009) represented a turning-point in human history (Kelekna, 2009). In addition to providing us with faster transportation, it also revolutionized warfare first with the development of chariotry in the early Bronze Age, some ~4000 years ago (Anthony and Brown, 2011) and 1200 years later, in the early Iron Age, with the emergence of mounted cavalry (Drews, 2004). Reconstructing the early stages of the horse domestication process on the basis of classical zooarchaeological proxies has been contentious in the absence of clear morphological changes before the Iron Age (Benecke and von den Driesch, 2003). Additionally, morphological variation in osseous assemblages that are frequently fragmentary is often not sufficient to determine hybrids and genders (Baxter, 1998). This has thus limited our capacity to track the onset of mule breeding (Schubert et al., 2017) and differential male and female management through space and time.

The application of methodologies at the forefront of ancient genomics to equine remains has, in the last few years, considerably enhanced our understanding of the horse domestication process, from its early stages to its most modern developments (see Orlando, 2019) for a recent review). This work uncovered the survival of divergent lineages in both Iberia and Siberia until at least the third millennium BCE (Before Common Era) (Fages et al., 2019; Gaunitz et al., 2018; Librado et al., 2015; Schubert

et al., 2014b). These now-extinct lineages were found to have had no significant contribution to the genetic makeup of modern domestic horses. Additionally, the earliest domestic horses known in the archaeological record and excavated from the Botai settlements of the northern Central Asian steppes, were found to belong to another lineage than that comprising all modern domestic horses (Gaunitz et al., 2018). In fact, they appeared directly ancestral to Przewalski's horses, which were previously considered as the last remaining truly wild horses living on the planet (Der Sarkissian et al., 2015). The ancient genome data currently available suggested that modern domestic horses developed from another genetic background within the third millennium BCE, either via another independent domestication, or through introgression capture, a process by which the original genetic source becomes diluted as the domestic stock expands and mixes with wild local populations (Larson and Fuller, 2014). Finally, the extensive ancient genome time-series generated thus far has also started to uncover how past breeders managed and transformed the available genetic resources in different (pre-)historical contexts by means of admixture, selection and stud formation (Fages et al., 2019; Librado et al., 2017). For example, recent work revealed that specific stallion lineages have increasingly participated in breeding for approximately ~2000 years (Fages et al., 2019; Wutke et al., 2018), in particular those Oriental stallion bloodlines that were especially favored during the Modern time period (Felkel et al., 2018; Wallner et al., 2017).

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The respective contributions of males and females in the different osseous assemblages made available for ancient DNA analyses have remained, however, overlooked. Yet, identifying the molecular sex of animal individuals requires minimal sequence data, and ancient DNA work has started to uncover important sex bias in the mammoth (Pečnerová et al., 2017), brown bear and bison (Gower et al., 2019) fossil records, possibly owing to differential behaviour and/or dispersal ranges between males and females. The control of horse reproduction resulting from domestication may also have introduced differential patterns of survival in males and females, following what seen in cattle, in which large proportions of male calves are culled. Additionally, social and/or ritual preferences as well as the restriction of specific working tasks to one gender only may have led to different occurrences of males and females in animal bone assemblages associated with anthropogenic contexts. This has been for example documented in Scythian Pazyryk funerary rituals, during which males were preferentially sacrificed (Lepetz, 2013; Librado et al., 2017), or in Viking Age graves (Nistelberger et al., 2019), also largely over-represented in horse males.

In this study, we monitored for the first time the male:female sex ratio in horse assemblages across time and tracked possible changes that may have been driven by human management. To achieve this, we complemented the ancient DNA time transect currently available for horses by generating shotgun sequence data for 19 Upper Paleolithic horses excavated in the Goyet (Germonpré, 1997) and Trou Magritte (Otte and Straus, 1996) caves, Belgium (Fig. 1). These provided sex ratio estimates prior to domestication. The sequence data previously generated for a total of 249 ancient horses (Table A1) allowed us to follow how male:female sex ratios evolved in the face of the domestication process (Fages et al., 2019; Gaunitz et al., 2018; Librado et al., 2015; Orlando et al., 2013; Schubert et al., 2014b).

2. Material & methods

2.1. Data generation

Drilling and DNA extraction were performed in the ancient DNA facilities of the GLOBE institute, formally known as the Centre for GeoGenetics, University of Copenhagen, Denmark. We extracted DNA from 178 to 570 mg of bone or tooth powder following the protocol described in (Yang et al., 1998) and modified by (Gamba et al., 2016), Table 1). In short, pulverized powder was pre-digested for one hour at 37 °C in 4 ml of a lysis buffer consisting of EDTA 0.45 M, Proteinase K 0.25 mg/ml and N-lauryl Sarcosyl 0.5%. The resulting pellet was then digested overnight at 42 °C in an identical fresh lysis buffer. The supernatant of the second digestion was recovered, concentrated and purified on Minelute columns (QIAGEN®). DNA extracts were incubated with USER™ enzyme mix (NEB®, 0.235 units/mL) at 37 °C for 3 h to limit the impact of post-mortem cytosine deamination, which are typical of ancient DNA (Briggs et al., 2007). We then built blunt-end double stranded genomic libraries following (Meyer and Kircher, 2010), as modified in (Gamba et al., 2016) and subjected a 1:20 dilution of each library to a quantitative real-time PCR (Polymerase Chain Reaction) on a Roche LightCycler 480 Real-Time PCR System to determine the adequate cycle number for library amplification. Subsequently, libraries were amplified by PCR for 9–16 cycles, as in (Gamba et al., 2016). Each PCR was performed in a total reaction volume of 25 µl, using 3 to 6 µl of library, 1 unit of AccuPrime™ Pfx DNA polymerase and custom forward and reverse PCR primers at 200 nM final molarity. Each reverse PCR primer was designed to contain a unique 6-nucleotide barcode used for sequence demultiplexing (Table 1). Libraries thus amplified and indexed were purified on Minelute columns (QIAGEN®), eluted in 25 µl of elution buffer (10 mM Tris-HCl, pH = 8.5 and 0.05% Tween) and quantified on a TapeStation 2200 instrument (Agilent Technologies). Finally, purified DNA libraries were pooled and sequenced on an Illumina HiSeq2500 platform at the Danish National High-Throughput DNA Sequencing Centre (Copenhagen, Denmark) using the Single-Read sequencing mode (80 or 100 cycles).

2.2. Data statistical analyses

The DNA sequences of each individual horse specimen were processed through the same computational pipeline aimed at (1) identifying high-quality alignments against the horse reference genome (EquCab2, (Wade et al., 2009)) and (2) determining the taxonomic status and gender. Both steps were carried out using PALEOMIX (Schubert et al., 2014a), in which DNA sequencing reads were first trimmed for adapter sequences and/or low-quality ends through AdapterRemoval2 (Schubert et al., 2016). They were subsequently aligned using BWA version 0.7.17 (Li and Durbin, 2009) with default parameters, except that seeding was disabled, then realigned using GATK (McKenna et al., 2010), and filtered for PCR duplicates using MarkDuplicates and for mapping quality scores strictly lower than 25 using samtools (Li et al., 2009). Sequence data aligned against the horse reference genome EquCab2 (Wade et al., 2009) are available on the European Nucleotide Archive (ENA): PRJEB38037.

Taxonomic status and sex were determined using Zonkey (Schubert et al., 2017), which is integrated within PALEOMIX (Schubert et al., 2014a), and shows maximal sensitivity and specificity as long as 1000–10,000 aligned sequences are available. This was the case for all individuals investigated in this study. Male:female sex ratios were calculated within time bins of 1000 years and considering a step value of 250 years. Confidence intervals per time bin were estimated assuming binomial sampling in R (R Core Team, 2013). Statistical significance for possible shifts in male:female sex ratios was tested within pre-defined time windows using a Fisher's exact test in R (R Core Team, 2013). For each time window, we also tested deviation from expected parity with a two-tailed binomial test. The different time windows considered for testing statistical significance were pre- and post-3200 years cal. BP to pre- and post-4600 years cal. BP, shifting time every 100 years. We next rejected that the geographic distributions of males and females were significantly different prior to domestication across Eurasia. To achieve this, we performed Kolmogorov-Smirnov tests on the latitude and longitude distributions independently, and a kernel test based on distances between all sites represented in the male and female subsets, available in R (R Core Team, 2013), as recently implemented by Gower and colleagues (Gower et al., 2019). Finally, we also confirmed that the fractions of endogenous DNA found in male and female samples were not significantly different using a Kolmogorov-Smirnov test in R (R Core Team, 2013). All figures were plotted in ggplot2 (Wickham, 2016) in R.

2.3. Sex assignment performance

The procedure underlying sex assignment in Zonkey builds on the expected difference in coverage between the autosomes and the X chromosome in males and females. More specifically, for each individual chromosome, the total number of nucleotide bases covered is normalized by the total length of the chromosome. If the normalized coverage obtained for the X chromosome is within the range observed across each individual autosome, the individual is suggested to be a female. It is suggested as male in the case the normalized coverage obtained for the X chromosome is approximately only half the range observed across each individual autosome. The assignment is however only suggestive and no further statistical test is performed. To quantify the performance of this procedure quantitatively, we have formalized a statistical test aimed at rejecting the two null hypotheses that the individual is a male (H0a), or a female (H0b). The test consists of building a contingency table comprising the coverage achieved on the autosomes and the X chromosome on the one hand, and the length of the autosomes and the X chromosome on the other hand. Then, a Chi-square test is applied and the p-values returned provide a measure of the strength of the rejection of both null hypotheses. Finally, the individual is assigned as male if the ratio of p-values returned for H0a and H0b is superior to 1,000,000 or as female if this ratio is inferior to 0.000001. The sex of the individual is left unassigned otherwise. The performance of this procedure was evaluated in one female

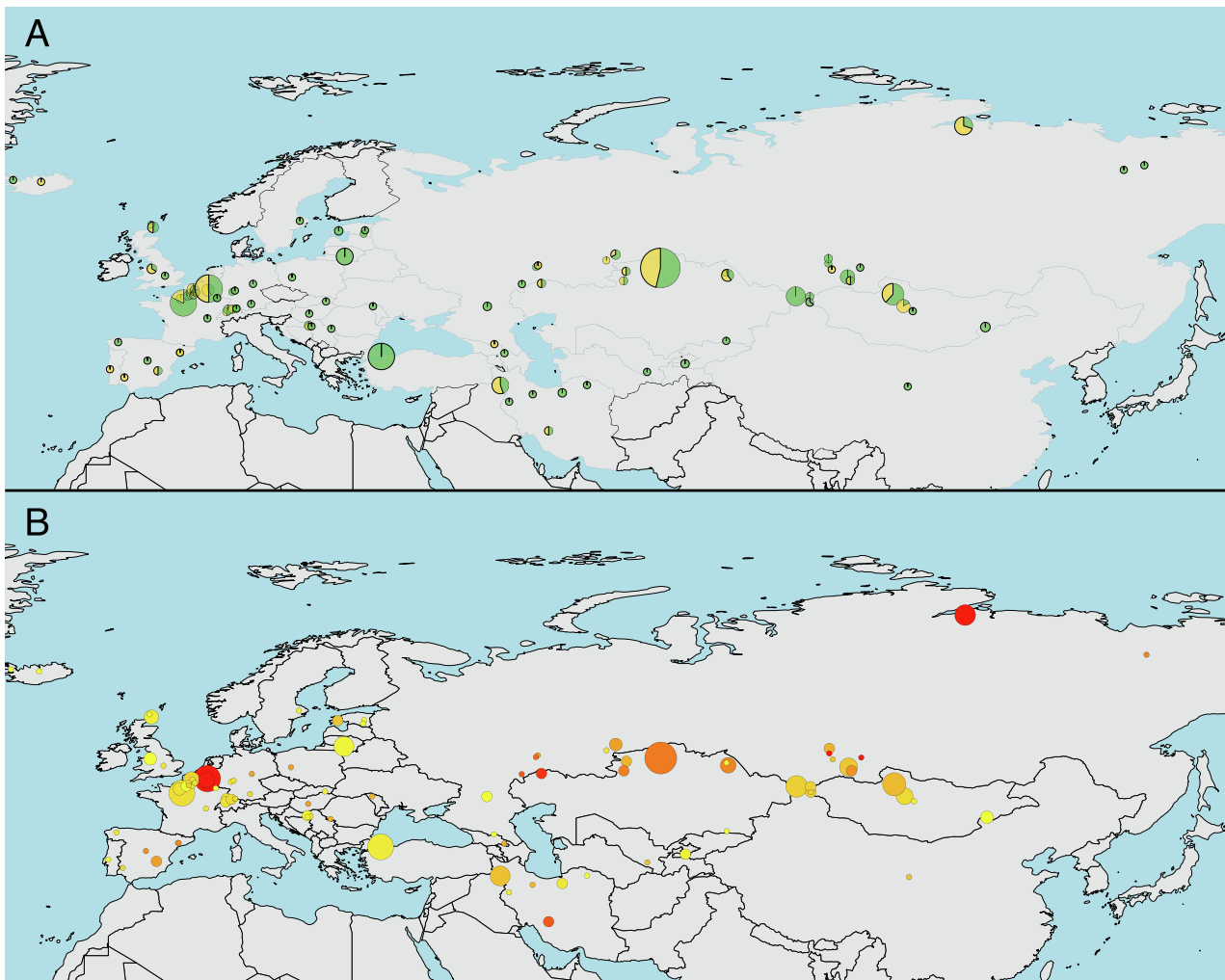


Fig. 1. Geographical distribution of horses included in this study. A. Geographical distribution of female and male horses. Pie charts are proportional to the total number of specimens excavated at each site. Gold refers to females and green to males. B. Temporal and geographical distribution of horses. Pie charts are proportional to the total number of specimens excavated at each site. The colour gradient indicates the average age of samples per site, from 0 (yellow) to 8000 years (red). Sites older than 8000 years are also shown in red.

individual by random sampling reads from the bam alignment filtered for mapping quality and PCR duplicates. The number of reads ranged from 100 to 5000, incrementing by values of one hundred until 2000 and then by values of 1000. The procedure was repeated for a male individual. The following tables (Table B1 and Table C1) provide the number of male and female assignments considering a total of 100 pseudo-replicates. Interestingly, the procedure returned positive predictive values, which consist of the ratio of True Positives and the sum of True Positives and False Positives, comprised between 97% and 100% as long as a minimum number of 800 reads were available for males. It was comprised between 93.8% and 100% for females as long as a minimum number of 900 reads were available. In the case that 3000 reads or more were available, the positive predictive value of this procedure was equal to 100%. We thus conclude that sub-optimal sex assignment can be achieved from approximately ~1000 reads (false-positive rate = 2% and false-negative rates = 1% for both males and females) and that full predictive power is obtained from approximately ~3000 reads for both sexes.

3. Results

Previous screening of ancient DNA preservation levels in horse bone samples excavated at Goyet, Belgium identified the presence of four females (Fages et al., 2019). In order to estimate male:female sex ratios in the Upper Palaeolithic of the region, we further extended the genetic analyses

to an additional number of 14 specimens from the same cave, and five specimens from Trou Magritte, which represents another neighbouring cave. DNA extracts were compatible with library building and generation of low-coverage sequence data for all 19 specimens (representing a total of 1,338,640–63,696,650 sequencing reads per individual, Table 2). Endogenous DNA levels provided sufficient read numbers to confirm all 19 samples as horses and to determine the molecular sex of each individual. Five new samples from Goyet and three samples from Trou Magritte were identified as females, while all other 11 specimens consisted of males. This provided a 11:12 (~0.92) male:female sex ratio for the Upper Palaeolithic of Belgium. This number indicated a more balanced male:female sex ratio than the 3:7 value obtained when applying the same computational procedure to previously published Upper Paleolithic horse data from the Taymyr peninsula, north-eastern Siberia, Russia (Orlando et al., 2013; Schubert et al., 2014b). Including two more Upper Palaeolithic horse remains from Kokorevo and Merzly Yar, two sites located in the south-western Siberian range, brought the male:female sex ratio to 5:7 (~0.71), on par with the results obtained in the Upper Palaeolithic of Belgium. This indicates no sex-bias amongst the horse bone assemblages pre-dating horse domestication (two-tailed binomial test, p -value = 0.736).

We next applied the same procedure to Neolithic and Eneolithic osseous remains for which sufficient amounts of sequencing reads were previously generated to confirm the specimens investigated as horses. At Botai, where the earliest evidence for horse domestication was reported (Outram et al.,

Table 1
Lab procedures performed on each sample sequenced in this study.

Sample name	Registration number	Powder (mg)	Extraction method	Digestion fraction	USER treatment	Library method	DNA polymerase	Amplification cycles	Index
Goyet_Vert273	CGG_1_018502	406	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	15	TTAGGC
Goyet_Vert275	CGG_1_018504	570	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	13	TGACCA
Goyet_Vert277	CGG_1_018506	304	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	15	ACAGTG
Goyet_Vert285	CGG_1_018514	280	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	13	ATACCT
Goyet_Vert287	CGG_1_018516	527	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	12	ATGAGC
TrouMagritie_Vert288	CGG_1_018517	200	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	9	ATGGTT
TrouMagritie_Vert289	CGG_1_018518	295	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	9	ATTAAA
TrouMagritie_Vert291	CGG_1_018520	426	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	13	CGGCAC
Goyet_Vert295	CGG_1_018524	514	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	14	GACTTG
Goyet_Vert297	CGG_1_018526	448	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	10	GATGCA
Goyet_Vert298	CGG_1_018527	473	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	11	GCCAAAT
Goyet_Vert301	CGG_1_018530	200	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	16	GCCAAAT
Goyet_Vert302	CGG_1_018531	490	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	13	CAGATC
Goyet_Vert303	CGG_1_018532	178	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	15	ACTTGA
Goyet_Vert305	CGG_1_018534	350	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	15	TAGCTT
Goyet_Vert308	CGG_1_018537	263	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	16	GTGTAT
Goyet_Vert312	CGG_1_018541	522	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	12	ACCATC
TrouMagritie_Vert331	CGG_1_018560	380	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	10	ATTCTC
TrouMagritie_Vert332	CGG_1_018561	455	Yang et al (1998), modified by Gamba et al (2016)	2nd	yes	Meyer and Kircher (2010)	Accuprime	9	CAAAAT

2009), we found no statistical support for unbalanced male:female sex ratios (15:13, ~1.15; two-tailed binomial test, p-value = 0.851). The same was true when including six older Eneolithic/Neolithic specimens from Russia (Lebyazhinka IV, Altata and Derkul) and Iran (Tepe Mehr Ali), which provided a male:female sex-ratio estimate of 19:15 (~1.17, two-tailed binomial test, p-value = 0.608). Likewise, extending the analyses to six horse males and seven females dated to 4500–5200 cal. BP confirmed the presence of statistically balanced sex-ratios between the first half of third millennium and the sixth millennium BCE (25:22, ~1.14; two-tailed binomial test, p-value = 0.771). Binning the remaining horse data that were previously published for 187 horses revealed highly unbalanced sex-ratios for the following time period (i.e. the last 4600 years), which included 146 males and 43 females (ratio ~3.48). This indicates a statistically significant over-representation of males in osseous horse assemblages from approximately 4600 years ago (binomial test, p-value = 2.57e-14).

The male:female sex-ratios estimated for all horse remains identified prior to and following 4500 years ago, or any subsequent century until 3200 years ago, also indicated a shift towards the presence of more males in osseous assemblages in the more recent past with ratios being significantly different prior to and after shift date (Table 3, Fisher's exact tests, p-values < 6e-5; two-tailed binomial tests, p-values < 7e-14). The lowest p-values were obtained for a shift date of 3900 years cal. BP (two-tailed binomial test, p-value = 3.75e-15; Fisher's exact test, p-value = 4.17e-6), suggesting a strong shift in animal gender representation occurred around this date.

This finding was confirmed when calculating male:female sex ratios within time bins of 1000 years and a step-size of 250 years (Fig. 2), as the earliest time bin for which confidence intervals did not intersect the 1:1 unbalanced expectation was 3450–4450 years cal. BP. This strongly suggests that the economic shifts associated with the early Bronze Age introduced a bias in the occurrence of males within horse osseous assemblages. Indeed, the adoption of Bronze metallurgy, as it necessitated work compartmentation and favoured the development of long-distance exchange of prestige goods, strongly contributed to the emergence of social stratification (Kristiansen and Rowlands, 2005), and hence to a social and symbolic distinction in the role of males and females in Eurasian cultures. The trend towards an over-representation of males was maintained in all subsequent 1000-year time bins (i.e. following 3450 years cal. BP, Fig. 2). This pattern held true even when excluding sites for which at least five horses but only one sex was identified (reduced dataset, Table 3, Fig. A1).

Additionally, we tested whether the geographical distribution of males and females prior and after 3900 years cal. BP could explain the male:female sex ratios observed. While the geographic dispersions of males and females prior to 3900 years cal. BP did not show any statistical difference (kernel test, p-value = 0.877), they appeared to be different after 3900 years cal. BP when taking all samples into account (kernel test, p-value = 0.003). As this is most likely due to the accumulation of sites where only males have been identified, we thus created a reduced dataset, filtered out all sites for which at least five horses but only one sex was identified. After excluding a total of four sites out of 72, geographic dispersions of males and females did not differ significantly (kernel test, p-value = 0.079). This rejected differential geographic dispersal in males and females as a potential cause for the observed sex-ratio bias. Finally, the distributions of endogenous DNA levels in males and females were also not found to be statistically different, ruling out sex-specific taphonomic bias as a possible driver (Kolmogorov-Smirnov test, p-value = 0.059). We also caution that cultural filtering in the types of excavated sites in Eurasia might introduce a bias in our dataset, but we hypothesize that this bias should be negligible considering the geographical and temporal diversity of the sites investigated in this study.

4. Discussion

In this study, we used low-coverage DNA sequence data to estimate the male:female sex ratios of horse osseous assemblages from the Upper Palaeolithic to the Modern period. We found a balanced representation of

Table 2
Sequencing summary statistics for each sample sequenced in this study.

Sample name	Registration number	Sequencing platform	Type of data	Retained reads	Hits	Endogenous fraction	Clonality	Coverage mtDNA	Coverage nuDNA
Goyet_Vert273	CGG_1_018502	HiSeq2500	shotgun	2,488,558	106,461	4.28%	7.57%	0.26	0.002
Goyet_Vert275	CGG_1_018504	HiSeq2500	shotgun	1,423,704	26,094	1.83%	1.61%	0.46	0.000
Goyet_Vert277	CGG_1_018506	HiSeq2500	shotgun	2,804,799	5874	0.21%	0.97%	0.02	0.000
Goyet_Vert285	CGG_1_018514	HiSeq2500	shotgun	5,400,140	6771	0.13%	2.01%	0.02	0.000
Goyet_Vert287	CGG_1_018516	HiSeq2500	shotgun	6,283,312	375,354	5.97%	2.03%	1.58	0.007
TrouMagrite_Vert288	CGG_1_018517	HiSeq2500	shotgun	8,562,409	2611	0.03%	0.73%	0.01	0.000
TrouMagrite_Vert289	CGG_1_018518	HiSeq2500	shotgun	3,750,626	2194	0.06%	0.55%	0.01	0.000
TrouMagrite_Vert291	CGG_1_018520	HiSeq2500	shotgun	4,830,630	29,720	0.62%	1.50%	0.58	0.001
Goyet_Vert295	CGG_1_018524	HiSeq2500	shotgun	1,338,640	5476	0.41%	0.37%	0.02	0.000
Goyet_Vert297	CGG_1_018526	HiSeq2500	shotgun	6,624,274	7424	0.11%	0.70%	0.02	0.000
Goyet_Vert298	CGG_1_018527	HiSeq2500	shotgun	3,387,325	43,821	1.29%	0.50%	0.09	0.001
Goyet_Vert301	CGG_1_018530	HiSeq2500	shotgun	2,388,392	48,899	2.05%	3.30%	0.43	0.001
Goyet_Vert302	CGG_1_018531	HiSeq2500	shotgun	6,070,341	6961	0.11%	2.01%	0.02	0.000
Goyet_Vert303	CGG_1_018532	HiSeq2500	shotgun	63,696,650	28,202	0.04%	33.43%	0.07	0.000
Goyet_Vert305	CGG_1_018534	HiSeq2500	shotgun	3,313,562	17,439	0.53%	3.72%	0.14	0.000
Goyet_Vert308	CGG_1_018537	HiSeq2500	shotgun	60,287,514	599,579	0.99%	51.22%	1.68	0.007
Goyet_Vert312	CGG_1_018541	HiSeq2500	shotgun	3,505,284	30,323	0.87%	1.77%	0.63	0.001
TrouMagrite_Vert331	CGG_1_018560	HiSeq2500	shotgun	6,651,565	70,252	1.06%	1.37%	0.12	0.001
TrouMagrite_Vert332	CGG_1_018561	HiSeq2500	shotgun	7,302,824	373,514	5.11%	1.31%	1.21	0.007

males and females throughout the Upper Palaeolithic and until ~3900 years ago. This includes the Eneolithic Botai site, where horses were reported to be both hunted and managed as herds (Outram et al., 2009). The unbiased sex ratios suggest no particular hunting preference for females by Upper Palaeolithic hunter gatherers but also during early stages of horse management. This is in striking contrast to what was recently reported in other herbivore megafaunal species such as the bison (Gower et al., 2019) and the woolly mammoth (Pečnerová et al., 2017), but also for the brown bear, for which the sex representation showed a strong excess of males during the late Pleistocene. The evidence for unbalanced sex ratios was interpreted to be the result of less risk-adverse behaviour and/or increased dispersal rates in males, whereby sexually mature bachelor males disperse while females remain clustered in their native herds. The even sex ratio observed here indicates that the social structure of horses, which naturally corresponds to herds dominated by a single reproductive stallion, did not impact the sexual representation of the fossil record.

The balanced representation of adult horse males and females at the Eneolithic Botai settlement provided important information about how male and female animals were managed during the earliest stages of domestication. Although criticism of the horse domestication at Botai has been levied based on mortality distributions, non-selective kill-patterns

and metacarpal measurements (Benecke and von den Driesch, 2003; Kosintsev, 2010; Kosintsev and Kuznetsov, 2013; Levine, 1999), independent lines of evidence in favour of domestication at Botai have accumulated over the years. These include the discovery of corral enclosures around Botai pit houses, and the identification of bit wear damage on molars and mare milk fatty acids in ceramics (Anthony and Brown, 2011; Olsen, 2006; Outram et al., 2009). Demographic reconstructions based on mitochondrial DNA variation have also suggested strongly declining stocks at the time Botai people established more secondary and larger villages with a subsistence model almost exclusively based on horses (Ganuitz et al., 2018). Current views therefore depict Botai horses as a mixture of horses managed for transportation and milking, and horses hunted for meat and hides. In particular, the isotopic signatures of fatty acids preserved on ceramics have supported the consumption of horse milk on site some ~5500 years ago (Outram et al., 2009). Despite milking, horse management did not seem to have relied on pronounced male foal culling, as the sex ratios calculated in this study on Botai specimens were balanced. Additionally, previous work indicated the absence of a Schlepp effect at Botai, supporting horse slaughtering on site (Olsen et al., 2006). The balanced sex ratios observed in this study demonstrate that horse meat was obtained equally from those males and

Table 3
p-values associated with different shift dates. The global dataset includes all 268 individuals included in this study; the reduced dataset excludes sites for which at least five horses but only one sex was identified, and consists of 224 individuals. The Fisher's exact test calculates whether male:female ratios are significantly different before and after shift date, while the two-tailed binomial tests whether distributions prior to and after shift date differ from a 1:1 male:female ratio.

shift date	Global dataset			Reduced dataset		
	Fisher's exact test	binomial two-tailed test pre-shift	binomial two-tailed test post-shift	Fisher's exact test	binomial two-tailed test pre-shift	binomial two-tailed test post-shift
4600 BP	3.68e-05	1	2.57e-14	0.0039	1	1.05e-06
4500 BP	3.68e-05	1	2.57e-14	0.0039	1	1.05e-06
4400 BP	2.24e-05	1	1.81e-14	0.0038	1	8.74e-07
4300 BP	2.24e-05	1	1.81e-14	0.0038	1	8.74e-07
4200 BP	2.24e-05	1	1.81e-14	0.0038	1	8.74e-07
4100 BP	2.24e-05	1	1.81e-14	0.0038	1	8.74e-07
4000 BP	2.80e-05	0.912	2.81e-14	0.0060	0.912	1.24e-06
3900 BP	4.17e-06	1	3.75e-15	0.0016	1	3.37e-07
3800 BP	1.13e-05	0.834	9.94e-15	0.0017	0.834	1.19e-07
3700 BP	1.13e-05	0.834	9.94e-15	0.0017	0.834	1.19e-07
3600 BP	1.13e-05	0.834	9.94e-15	0.0017	0.834	1.19e-07
3500 BP	2.49e-05	0.688	2.46e-14	0.0073	0.688	1.70e-06
3400 BP	2.49e-05	0.688	2.46e-14	0.0073	0.688	1.70e-06
3300 BP	2.49e-05	0.688	2.46e-14	0.0073	0.688	1.70e-06
3200 BP	5.26e-05	0.538	6.05e-14	0.0116	0.538	3.46e-06

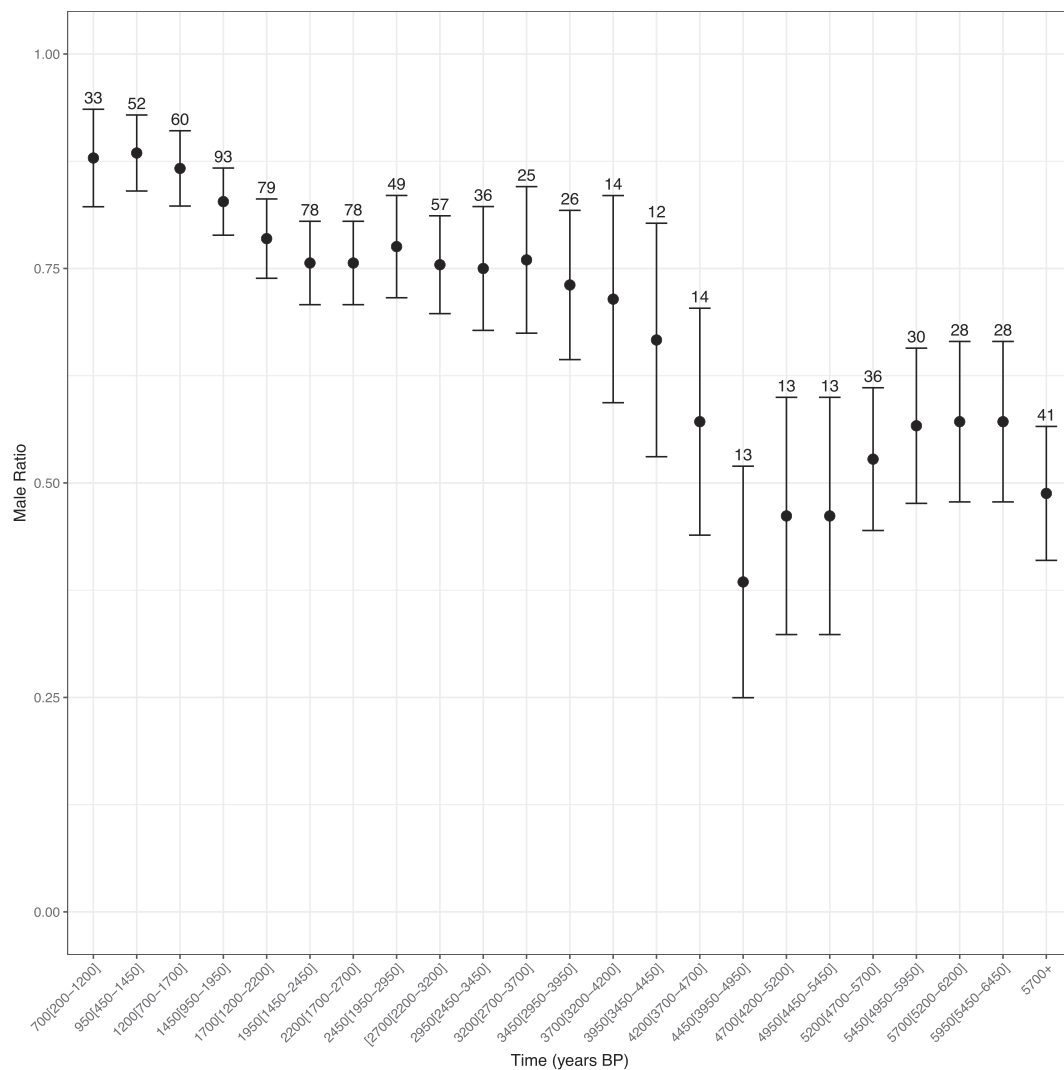


Fig. 2. Evolution of male ratios through time. Error bars indicate standard deviations from binomial distributions, figures above error bars indicate the number of samples in each bin.

females slaughtered on site. Furthermore, demographic reconstructions based on Bayesian skyline plots and tip-dated whole mitochondrial genomes indicated declining horse stocks during the Eneolithic (Gaunitz et al., 2018). This suggested that Botai people may have started managing horses to maintain access to a resource that was essential to their subsistence economy, in line with the expectations of prey-domestication pathways described in (Zeder, 2012). The absence of biased sex ratios observed in our study likely indicates that the exploitation of both horse male and female carcasses ensured that sufficient meat was acquired.

The time period around ~3900 years ago marked a drastic shift in male:female sex ratios inferred from excavated remains, after which the horse osteological record comprises approximately four males for every female (Fig. 2). This over-representation of horse males was maintained when disregarding those animals excavated from ritual burial sites (77/25 ~ 3.08 males for every female) and even more pronounced in the animal bones found in funerary contexts (66/14 ~ 4.71 males for every female). This indicates that the status of male and female horses dramatically changed during the Bronze Age period. This is in line with archaeozoological evidence from the Late Bronze Age cemeteries of the Volga-Ural region associated with the Sintashta, Potapovka and Petrovka cultures, that suggest a domination of male horses in funerary rates (Kosintsev, 2010). Interestingly, this pattern somehow mirrors that observed in humans, for whom a clear binary gender structure ubiquitous across all funerary practices, clothing, personal ornaments and

representations is not observed during the Neolithic but became the norm from the transition between the Neolithic and the Bronze Age onwards (Robb and Harris, 2018). In addition, the prevalence of male horses in funerary contexts throughout the past three millennia is in line with archaeological evidence from burial sites (Bertašius and Daugnora, 2001; Taylor, 2017) and suggests that stallions (or geldings) were more prized for sacrificial rituals. This is possibly due to symbolic attributes then-associated with masculinity, mounted warriors and chariotry, such as power, protection and strength (Frie, 2018). In particular, petroglyph images associated with vehicles, characterized by two wheels with spokes, became typical by the late third – early second millennium BCE (Jacobson-Tepfer, 2012). They are generally associated with male warriors and the emergence of mobile warfare (Anthony, 2007) or ritual needs, in particular the passage to the after-life land (Jones-Bley, 2000). This suggests an essential ideological role of stallions and their use in elite warfare and ritual practices (Drews, 2004; Kelekna, 2009; Novozhenov and Rogozhonskiy, 2019).

5. Conclusion

The analysis of genome data from 268 ancient horses showed that unlike other herbivorous megafaunal species, males were not over-represented in the Upper Palaeolithic horse fossil record, suggesting that horse dimorphic behavior and social herd structure most likely did not impact on their taphonomy. We further found that the male:female sex

ratio stayed steady until ~3900 years cal. BP, including at Botai, which indicates that early horse herding practices introduced no particular preference for one sex. However, we noted a striking prevalence of males in archaeological horse bone assemblages over the last ~3900 years, which is concomitant with human representations and funeral practices becoming systematically gendered. Future research should focus on assessing the molecular sex of horses from Early and Middle Bronze Age Pit Grave and Catacomb cultures, which do show evidence for social inequality, but for which sex inequalities remain to be investigated. Regardless, our observations show that the emergence of a gendered vision of the world in the Bronze Age also extended to the domestic animal sphere. Whether this only applies to the horse, as the animal of prestige by excellence, or also extends to other domestic animals, such as dogs, pigs and cattle, remains to be investigated.

CRedit authorship contribution statement

Antoine Fages: Conceptualization, Methodology, Validation,

Appendices

Formal analysis, Investigation, Data curation, Visualization, Writing - original draft, Writing - review & editing, Supervision, Project administration. **Andaine Seguin-Orlando:** Resources, Writing - original draft. **Mietje Germonpré:** Resources, Writing - original draft. **Ludovic Orlando:** Conceptualization, Methodology, Software, Validation, Formal analysis, Resources, Investigation, Data curation, Writing - original draft, Writing - review & editing, Funding acquisition.

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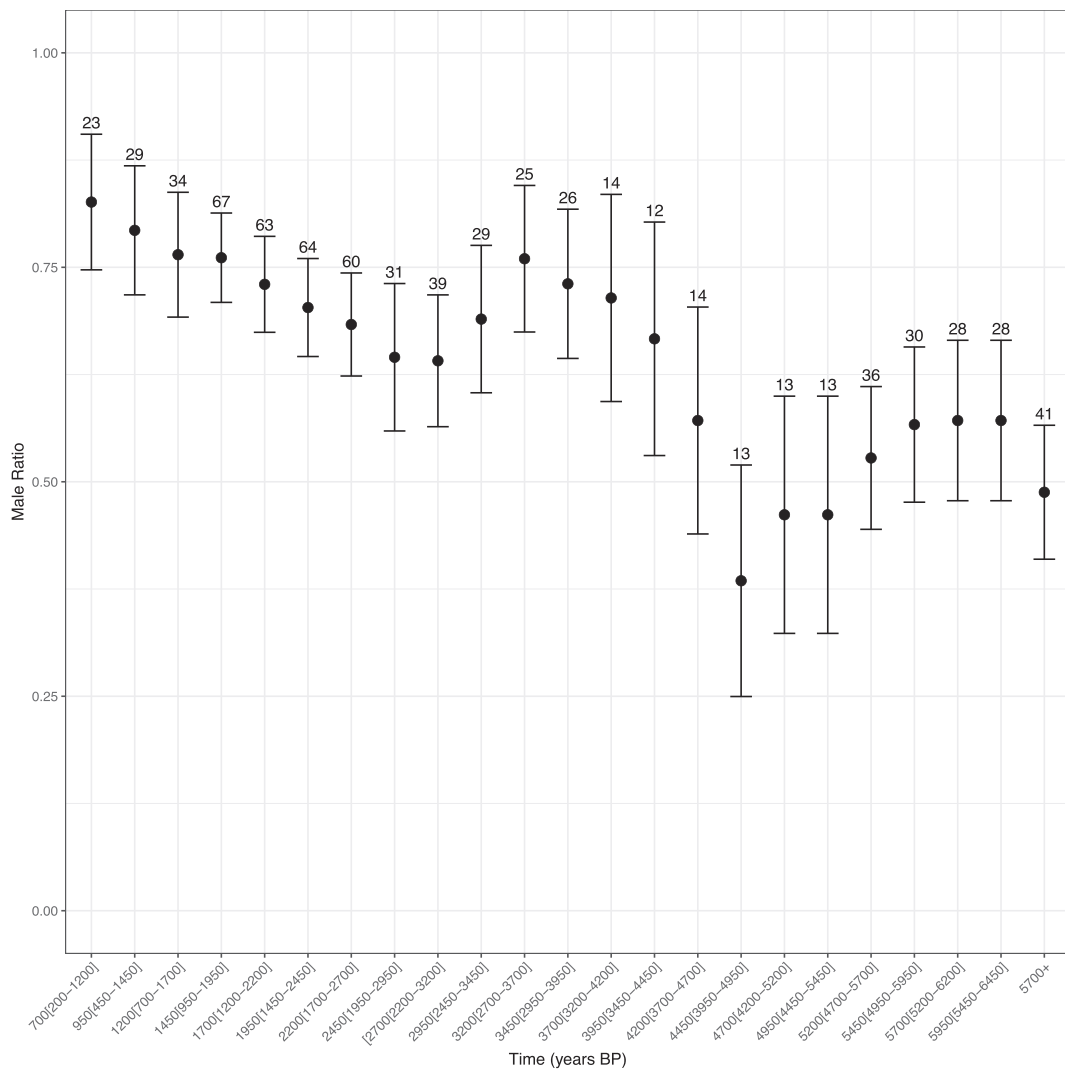


Fig. A1. Evolution of male ratios through time for the reduced dataset. The reduced dataset excludes sites for which at least five horses but only one sex was identified, and consists of 224 individuals. Error bars indicate standard deviations from binomial distributions, figures above error bars indicate the number of samples in each bin.

Table A1 Archaeological, cultural and geographical information relating to the 268 horses included in this study. (provided as excel file).

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Actiparc_GVA307	CGG_1_019857	Iron Age	2060	2060	male	horse	Actiparc	France	50.315	2.822	Fages et al. 2019	47.0%	
Actiparc_GVA308	CGG_1_019858	Iron Age	2245	2245	female	horse	Actiparc	France	50.315	2.822	Fages et al. 2019	58.6%	
Actiparc_GVA310	CGG_1_019860	Iron Age	2252	2252	female	horse	Actiparc	France	50.315	2.822	Gaunitz et al. 2018	62.7%	
Actiparc_GVA311	CGG_1_019861	Iron Age	2186	2186	male	horse	Actiparc	France	50.315	2.822	Fages et al. 2019	70.3%	
Actiparc_GVA309	CGG_1_019859	Iron Age	2235	2235	male	horse	Actiparc	France	50.315	2.822	Fages et al. 2019	72.6%	
Actiparc_GVA124	CGG_1_019382	Iron Age	2076	2076	male	horse	Actiparc	France	50.315	2.822	Fages et al. 2019	73.4%	
Santarem_254	CGG_1_020032	Middle Ages	750–1150	950	female	horse	Alcáçova de Santarém	Portugal	39.241	–8.692	Fages et al. 2019	15.4%	
Altata_NB31	CGG_1_017023	Neolithic/ Copper Age (5th mill.BCE)	6000–7000	6500	male	horse	Altata	Russia	51.07	48.44	Fages et al. 2019	12.6%	
ArzhanI_K3	CGG_1_017088	Iron Age	2660	2660	male	horse	Arzhan I	Russia	52.059	93.604	Librado et al. 2017	35.5%	x
ArzhanI_Arz3	CGG_1_017089	Iron Age	2650–2750	2700	male	horse	Arzhan I	Russia	52.059	93.604	Fages et al. 2019	40.5%	x
ArzhanI_K2	CGG_1_017079	Iron Age	2660	2660	male	horse	Arzhan I	Russia	52.059	93.604	Librado et al. 2017	58.3%	x
ArzhanII_Rus11	CGG_1_019162	Iron Age	2500	2500	male	horse	Arzhan II	Russia	52.059	93.604	Fages et al. 2019	25.1%	x
ArzhanII_Rus9	CGG_1_019160	Iron Age	2500	2500	male	horse	Arzhan II	Russia	52.059	93.604	Fages et al. 2019	38.7%	x
ArzhanII_Arz15	CGG_1_017084	Iron Age	2550–2600	2575	male	horse	Arzhan II	Russia	52.059	93.604	Fages et al. 2019	59.6%	x
ArzhanII_Arz17	CGG_1_017086	Iron Age	2550–2600	2575	male	horse	Arzhan II	Russia	52.059	93.604	Fages et al. 2019	62.9%	x
AugustaRaurica_JG160	CGG_1_019246	Roman period	1650–1850	1750	male	horse	Augusta Raurica - Insula 8	Switzerland	47.533	7.722	Fages et al. 2019	37.3%	
AugustaRauricaSchmidmatt_NBxP9261	CGG_1_020506	Roman period	1610–1820	1715	male	horse	Augusta Raurica - Schmidmatt	Switzerland	47.536	7.722	Fages et al. 2019	12.0%	
AugustaRauricaSchmidmatt_NBxK9279	CGG_1_020505	Roman period	1550–1750	1650	male	horse	Augusta Raurica - Schmidmatt	Switzerland	47.536	7.722	Fages et al. 2019	20.7%	
Balagansk_Rus19	CGG_1_019169	Iron Age	1750–2150	1950	male	horse	Balagansk	Russia	47.667	8.85	Fages et al. 2019	5.91%	
BapskaGradac_BAPSKA	CGG_1_020443	Middle Ages	1238	1238	male	horse	Bapska Gradac	Croatia	45.197	19.262	Fages et al. 2019	74.1%	
Batagai	N/A	Wild archaic	5088	5088	male	horse	Batagai	Russia	67.567	134.767	Librado et al. 2015	38.2%	
Batani_Rus14	CGG_1_019164	Bronze Age	3251	3251	male	horse	Batani	Russia	54.624	90.945	Gaunitz et al. 2018	33.8%	
Batani_Rus16	CGG_1_019166	Bronze Age	3283	3283	male	horse	Batani	Russia	54.624	90.945	Fages et al. 2019	55.1%	
Beauvais_GVA122	CGG_1_019380	Early Modern period	250–450	350	male	horse	Beauvais, la Maladrerie Saint-Lazare	France	49.415	2.101	Fages et al. 2019	78.4%	
Beauvais_GVA375	CGG_1_019925	Early Modern period	350–450	400	male	horse	Beauvais, Villiers-de-l'Isle-Adam	France	49.415	2.101	Fages et al. 2019	75.5%	

Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Belgheis_TrBWBX116	CGG_1_019521	Early Modern period	418	418	male	horse	Belgheis	Iran	37.042	57.472	Fages et al. 2019	68.2%	
Belkaragay_NB15	CGG_1_017007	Copper Age (late 4th mill. BC)	5000–5400	5200	female	horse	Belkaragay	Kazakhstan	51.52	62.55	Fages et al. 2019	12.3%	
Belkaragay_NB13	CGG_1_017005	Copper Age (late 4th mill. BC)	5000–5400	5200	male	horse	Belkaragay	Kazakhstan	51.52	62.55	Fages et al. 2019	14.6%	
Berel_BER11_L	CGG_1_016178	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	16.8%	x
Berel_BER08_H	CGG_1_016175	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	22.0%	x
Berel_BER10_K	CGG_1_016177	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	24.4%	x
Berel_BER07_G	CGG_1_016174	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	30.5%	x
Berel_BER04_D	CGG_1_016171	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	40.1%	x
Berel_BER01_A	CGG_1_016168	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	42.1%	x
Berel_BER05_E	CGG_1_016172	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	42.6%	x
Berel_BER09_I	CGG_1_016176	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	49.2%	x
Berel_BER06_F	CGG_1_016173	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	49.6%	x
Berel_BER12_M	CGG_1_016179	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	49.9%	x
Berel_BER02_B	CGG_1_016169	Iron Age	2300	2300	male	horse	Berel'	Kazakhstan	49.374	86.427	Librado et al. 2017	67.7%	x
Berufjordur_VHR102	CGG_1_020961	Middle Ages	850–1150	1000	male	horse	Berufjordur	Iceland	65.53	-22.117	Fages et al. 2019	21.3%	x
Borly4_PAVH4	CGG_1_018157	Copper Age	4907	4907	female	horse	Borly 4	Kazakhstan	52.287	76.967	Gaunitz et al. 2018	67.6%	
Borly4_PAVH8	CGG_1_018165	Copper Age	4911	4911	male	horse	Borly 4	Kazakhstan	52.287	76.967	Gaunitz et al. 2018	67.9%	
Borly4_PAVH9	CGG_1_018167	Copper Age	4910	4910	male	horse	Borly 4	Kazakhstan	52.287	76.967	Gaunitz et al. 2018	70.2%	
Borly4_PAVH11	CGG_1_018171	Copper Age	4948	4948	female	horse	Borly 4	Kazakhstan	52.287	76.967	Gaunitz et al. 2018	71.0%	
Borly4_PAVH6	CGG_1_018161	Copper Age	4945	4945	female	horse	Borly 4	Kazakhstan	52.287	76.967	Gaunitz et al. 2018	74.1%	
Botai_N	CGG_1_020194	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	2.91%	
Botai_NB18	CGG_1_017010	Copper Age	4625	4625	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	3.12%	
Botai_E	CGG_1_020185	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	7.12%	
Botai_D2	CGG_1_020205	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	10.2%	
Botai_O	CGG_1_020195	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	10.6%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Botai_T	CGG_1_020200	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	25.4%	
Botai_8	CGG_1_020179	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	40.4%	
Botai_D5	CGG_1_020208	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	44.3%	
Botai_D1	CGG_1_020204	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	57.4%	
Botai_D6	CGG_1_020209	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	58.3%	
Botai_D4	CGG_1_020207	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	61.0%	
Botai_F	CGG_1_020186	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	62.9%	
Botai_C	CGG_1_020183	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	68.0%	
Botai_L	CGG_1_020192	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	68.2%	
Botai_P	CGG_1_020196	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	68.6%	
Botai_K	CGG_1_020189	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	69.6%	
Botai_A	CGG_1_020181	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	69.8%	
Botai_3	CGG_1_018175	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	70.0%	
Botai_1	CGG_1_018173	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	71.6%	
Botai_G	CGG_1_020187	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	71.6%	
Botai_4	CGG_1_018176	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	72.6%	
Botai_R	CGG_1_020198	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	72.6%	
Botai_5	CGG_1_018177	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	72.7%	
Botai_Petrous	CGG_1_020210	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	73.2%	
Botai_I	CGG_1_020188	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	73.9%	
Botai_B	CGG_1_020182	Copper Age	5500	5500	female	horse	Botai	Kazakhstan	53.304	67.646	Fages et al. 2019	74.5%	
Botai_2	CGG_1_018174	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	74.7%	
Botai_6	CGG_1_018178	Copper Age	5500	5500	male	horse	Botai	Kazakhstan	53.304	67.646	Gaunitz et al. 2018	74.9%	
Boves_GVA191	CGG_1_019765	Roman period	1550–1750	1650	female	horse	Boves, chemin de Glisy	France	49.853	2.397	Fages et al. 2019	71.9%	
BozAdyr_KYRH10	CGG_1_018031	Middle Ages	1200	1200	male	horse	Boz-Adyr	Kyrgyzstan	39.998	71.073	Fages et al. 2019	71.7%	x
BozAdyr_KYRH8	CGG_1_018029	Middle Ages	1200	1200	male	horse	Boz-Adyr	Kyrgyzstan	39.998	71.073	Fages et al. 2019	74.3%	x

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
BroughOfDeerness_VHR010	CGG_1_020949	Middle Ages	1250–1450	1350	female	horse	Brough Of Deerness	United Kingdom	58.964	-2.705	Fages et al. 2019	68.7%	
BroughOfDeerness_VHR011	CGG_1_020950	Middle Ages	1250–1350	1300	male	horse	Brough Of Deerness	United Kingdom	58.964	-2.705	Fages et al. 2019	73.6%	
BroughOfDeerness_VHR037	CGG_1_020957	Middle Ages	1250–1450	1350	male	horse	BroughOfDeerness	United Kingdom	58.964	-2.705	Fages et al. 2019	22.6%	
BroughOfDeerness_VHR062	CGG_1_020959	Middle Ages	1250–1450	1350	female	horse	BroughOfDeerness	United Kingdom	58.964	-2.705	Fages et al. 2019	34.4%	
Bruszcewo_Bru4	CGG_1_018376	Bronze Age	3550–4150	3850	male	horse	Bruszcewo	Poland	52.007	16.562	Fages et al. 2019	1.91%	
CaminoDeLasYeseras_CdY2	CGG_1_018391	Copper Age	4429–4794	4611	male	horse	Camino de las Yeseras, Madrid	Spain	40.442	-3.494	Fages et al. 2019	22.1%	
Cantorella_UE2275x2	CGG_1_020989	Copper Age	4724	4724	female	horse	Cantorella	Spain	41.553	1.039	Fages et al. 2019	36.9%	
Capote_Cap102	CGG_1_016984	Bronze Age	2050–2150	2100	female	horse	Capote	Spain	38.098	-6.693	Fages et al. 2019	6.08%	
Chartres_GVA53	CGG_1_019311	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	57.0%	
Chartres_GVA112	CGG_1_019370	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	59.8%	
Chartres_GVA56	CGG_1_019314	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	62.7%	
Chartres_GVA9	CGG_1_019267	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	67.6%	
Chartres_GVA111	CGG_1_019369	Roman period	1850	1850	female	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	69.6%	
Chartres_GVA47	CGG_1_019305	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	70.6%	
Chartres_GVA60	CGG_1_019318	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	72.7%	
Chartres_GVA26	CGG_1_019284	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	72.9%	
Chartres_GVA81	CGG_1_019339	Roman period	1850	1850	female	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	73.8%	
Chartres_GVA75	CGG_1_019333	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	74.1%	
Chartres_GVA36	CGG_1_019294	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	74.7%	
Chartres_GVA43	CGG_1_019301	Roman period	1850	1850	female	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	74.8%	
Chartres_GVA28	CGG_1_019286	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	75.2%	
Chartres_GVA1	CGG_1_019259	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	75.3%	
Chartres_GVA115	CGG_1_019373	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	75.6%	
Chartres_GVA48	CGG_1_019306	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	76.0%	
Chartres_GVA4	CGG_1_019262	Roman period	1850	1850	male	horse	Chartres, boulevard de la Courtille	France	48.442	1.494	Fages et al. 2019	77.1%	
Dangstetten_R13DA	CGG_1_017519	Roman period	1959–1965	1962	female	horse	Dangstetten	Germany	47.5889	8.3108	Schubert et al. 2017	0.09%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Dangsteitlen_R10DA	CGG_1_017516	Roman period	1959–1965	1962	male	horse	Dangsteitlen	Germany	47.5889	8.3108	Schubert et al. 2017	0.25%	
Dariali_Georgia2	CGG_1_020266	Early Modern period	50–550	300	female	horse	Dariali, Tamara Fort	Georgia	42.74	44.62	Fages et al. 2019	60.8%	
Derkul_NB2	CGG_1_016994	Neolithic (6th mill. BCE)	7000–8000	7500	male	horse	Derkul	Russia	51.16	51.17	Fages et al. 2019	2.69%	
Derkul_NB4	CGG_1_016996	Neolithic (6th mill. BCE)	7000–8000	7500	female	horse	Derkul	Russia	51.16	51.17	Fages et al. 2019	19.6%	
Dunaujvaros_Duk2	CGG_1_018386	Bronze Age	4010	4010	male	horse	Dunaujváros	Hungary	46.962	18.936	Gaunitz et al. 2018	16.8%	
ElAcequion_Spain39	CGG_1_020485	Bronze Age	3926	3926	male	horse	El Acequión	Spain	39.024	–2.028	Fages et al. 2019	8.60%	
ElAcequion_Spain38	CGG_1_020484	Bronze Age	3991	3991	female	horse	El Acequión	Spain	39.024	–2.028	Fages et al. 2019	15.2%	
ElsVilars_UE4618	CGG_1_020962	Iron Age	2605	2605	female	horse	Els Vilars	Spain	41.57	0.95	Fages et al. 2019	61.0%	
Evreux_GVA140	CGG_1_019714	Roman period	1650–1850	1750	male	horse	Evreux, Clos-au-Duc	France	49.02	1.159	Fages et al. 2019	70.1%	x
Evreux_GVA133	CGG_1_019707	Roman period	1650–1850	1750	male	horse	Evreux, Clos-au-Duc	France	49.02	1.159	Fages et al. 2019	73.7%	x
Evreux_GVA135	CGG_1_019709	Roman period	1650–1850	1750	male	horse	Evreux, Clos-au-Duc	France	49.02	1.159	Fages et al. 2019	74.7%	x
Fengtai_Fer4	CGG_1_018396	Iron Age	2753	2753	male	horse	Fengtai	China	36.841	101.958	Fages et al. 2019	16.3%	
FrankfurtHedderheim_Fr1	CGG_1_018151	Roman period	1796	1796	male	horse	Frankfurt-Heddenheim	Germany	50.161	8.642	Fages et al. 2019	73.6%	
Fmонтаuban_GVA126	CGG_1_019384	Roman period	1805	1805	male	horse	Fresnes-lès-Montauban	France	50.3336	2.9319	Gaunitz et al. 2018	72.1%	x
Garbovat_Gar3	CGG_1_018389	Bronze Age	3507	3507	male	horse	Garbovat	Romania	44.867	22.008	Gaunitz et al. 2018	16.6%	
GolModII_Mon25	CGG_1_018061	Iron Age	1944	1944	female	horse	Gol Mod II	Mongolia	48.018	101.353	Fages et al. 2019	44.1%	x
GolModII_Mon24	CGG_1_018060	Iron Age	1926	1926	female	horse	Gol Mod II	Mongolia	48.018	101.353	Fages et al. 2019	70.8%	x
GolModII_Mon27	CGG_1_018063	Iron Age	1944	1944	female	horse	Gol Mod II	Mongolia	48.018	101.353	Fages et al. 2019	71.4%	x
GolModII_Mon26	CGG_1_018062	Iron Age	1921–1944	1932	female	horse	Gol Mod II	Mongolia	48.018	101.353	Fages et al. 2019	71.5%	x
GolModII_Mon23	CGG_1_018059	Iron Age	1940	1940	female	horse	Gol Mod II	Mongolia	48.018	101.353	Fages et al. 2019	73.3%	x
GolModII_Mon28	CGG_1_018064	Iron Age	1921	1921	male	horse	Gol Mod II	Mongolia	48.018	101.353	Gaunitz et al. 2018	73.4%	x
Goyet_Vert304	CGG_1_018533	Upper Palaeolithic	N/A	N/A	female	horse	Goyet	Belgium	50.447	5.009	Fages et al. 2019	2.28%	
Goyet_Vert300	CGG_1_018529	Upper Palaeolithic	31,750	31,750	female	horse	Goyet	Belgium	50.447	5.009	Fages et al. 2019	3.45%	
Goyet_Vert293	CGG_1_018522	Upper Palaeolithic	N/A	N/A	female	horse	Goyet	Belgium	50.447	5.009	Fages et al. 2019	5.58%	
Goyet_Vert311	CGG_1_018540	Upper Palaeolithic	35,803	35,803	female	horse	Goyet	Belgium	50.447	5.009	Fages et al. 2019	35.7%	
Goyet_Vert303	CGG_1_018532	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A1	Belgium	50.447	5.009	this study	0.04%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Goyet_Vert302	CGG_1_018531	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A1	Belgium	50.447	5.009	this study	0.11%	
Goyet_Vert305	CGG_1_018534	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A1	Belgium	50.447	5.009	this study	0.53%	
Goyet_Vert312	CGG_1_018541	Upper Palaeolithic	N/A	N/A	female	horse	Goyet A1	Belgium	50.447	5.009	this study	0.87%	
Goyet_Vert308	CGG_1_018537	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A1	Belgium	50.447	5.009	this study	0.99%	
Goyet_Vert301	CGG_1_018530	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A1	Belgium	50.447	5.009	this study	2.05%	
Goyet_Vert297	CGG_1_018526	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A2	Belgium	50.447	5.009	this study	0.11%	
Goyet_Vert295	CGG_1_018524	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A2	Belgium	50.447	5.009	this study	0.41%	
Goyet_Vert298	CGG_1_018527	Upper Palaeolithic	N/A	N/A	female	horse	Goyet A2	Belgium	50.447	5.009	this study	1.29%	
Goyet_Vert285	CGG_1_018514	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A3	Belgium	50.447	5.009	this study	0.13%	
Goyet_Vert277	CGG_1_018506	Upper Palaeolithic	N/A	N/A	male	horse	Goyet A3	Belgium	50.447	5.009	this study	0.21%	
Goyet_Vert275	CGG_1_018504	Upper Palaeolithic	N/A	N/A	female	horse	Goyet A3	Belgium	50.447	5.009	this study	1.83%	
Goyet_Vert273	CGG_1_018502	Upper Palaeolithic	N/A	N/A	female	horse	Goyet A3	Belgium	50.447	5.009	this study	4.28%	
Goyet_Vert287	CGG_1_018516	Upper Palaeolithic	N/A	N/A	female	horse	Goyet A3	Belgium	50.447	5.009	this study	5.97%	
Granastadir_VHR031	CGG_1_020955	Middle Ages	850–1150	1000	female	horse	Granastadir	Iceland	65.268	–18.24	Fages et al. 2019	7.80%	
Gregorevka4_PAVH2	CGG_1_018154	Middle Ages	1125	1125	male	horse	Gregorevka 4	Kazakhstan	52.629	76.739	Gaunitz et al. 2018	75.7%	x
Halvai_KSH5	CGG_1_017099	Bronze Age	2150–2800	2475	male	horse	Halvai 3	Kazakhstan	52.843	62.903	Fages et al. 2019	66.8%	x
Halvai_KSH4	CGG_1_017098	Bronze Age	3750–4150	3950	female	horse	Halvai 5	Kazakhstan	52.843	62.903	Fages et al. 2019	38.6%	x
Hauinstetten_1979	CGG_1_017139	Roman period	1912	1912	male	horse	Hauinstetten	Germany	48.308	10.894	Gaunitz et al. 2018	63.8%	x
Khatuu_Kha2_t1	CGG_1_018909	Iron Age	2245	2245	male	horse	Khatuu 2	Mongolia	48.583	88.394	Fages et al. 2019	17.6%	x
Khoront_UCIE2012x85	CGG_1_018038	Middle Ages	1224	1224	male	horse	Khoront	Mongolia	47.306	102.646	Fages et al. 2019	76.1%	x
Kokorevo_Rus3	CGG_1_019154	Upper Palaeolithic	14,450	14,450	male	horse	Kokorevo	Russia	53.933	90.933	Fages et al. 2019	8.10%	
KrasnayaGorka_Rus48	CGG_1_019195	Middle Ages	1379	1379	male	horse	Krasnaya Gorka	Russia	51.539	94.009	Fages et al. 2019	10.9%	x
Krasnokamenka_NB9	CGG_1_017001	Copper Age	4500	4500	female	horse	Krasnokamenka	Russia	54.35	60.15	Fages et al. 2019	9.49%	
Krasnokamenka_NB10	CGG_1_017002	Copper Age	4500	4500	male	horse	Krasnokamenka	Russia	54.35	60.15	Fages et al. 2019	12.2%	
KulianCave_MV178	CGG_1_020446	Sassanid period	1627	1627	female	horse	Kulian Cave	Iran	34.73	46.672	Fages et al. 2019	65.5%	
LebyazhinkaIV_NB35	CGG_1_017027	Copper Age(end of 5th mill. BCE)	6000–6400	6200	male	horse	Lebyazhinka IV	Russia	53.43	50.4	Fages et al. 2019	6.41%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
LongueilAnnel_GVA129	CGG_1_019387	Early Modern period	150–250	200	male	horse	Longueil-Annel	France	49.469	2.861	Fages et al. 2019	74.2%	
Macon_GVA201	CGG_1_019775	Roman period	1650–1750	1700	male	horse	Macon, rue Rambuteau	France	46.308	4.823	Fages et al. 2019	72.4%	
Mainz_Mzr1	CGG_1_018150	Middle Ages	1306	1306	male	horse	Mainz	Germany	49.99	8.26	Fages et al. 2019	73.3%	
Marvele_27	CGG_1_019414	Middle Ages	1020–1122	1071	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	6.38%	x
Marvele_22	CGG_1_019409	Middle Ages	1020–1122	1071	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	7.49%	x
Marvele_2	CGG_1_019389	Middle Ages	1020–1122	1071	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	11.7%	x
Marvele_5	CGG_1_019392	Middle Ages	1020–1122	1071	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	14.5%	x
Marvele_16	CGG_1_019403	Middle Ages	1020–1122	1071	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	16.8%	x
Marvele_1	CGG_1_019388	Middle Ages	1020–1122	1071	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	58.9%	x
Marvele_18	CGG_1_019405	Middle Ages	1122	1122	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	72.1%	x
Marvele_21	CGG_1_019408	Middle Ages	1020	1020	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	74.9%	x
Marvele_32	CGG_1_019419	Middle Ages	1077	1077	male	horse	Marvele cemetery	Lithuania	54.897	23.872	Fages et al. 2019	75.0%	x
MerzlyYar_Rus45	CGG_1_019192	Upper Palaeolithic	23,722	23,722	male	horse	Merzly Yar	Russia	53.363	95.363	Fages et al. 2019	59.4%	
Metz_GVA321	CGG_1_019871	Early Modern period	400–500	425	male	horse	Metz, Place de la République	France	49.115	6.173	Fages et al. 2019	72.3%	x
Micturin_Mic2	CGG_1_018388	Bronze Age	2950–3450	3200	male	horse	Micturin	Moldova	47.987	27.79	Fages et al. 2019	19.9%	
Noyon_GVA123	CGG_1_019381	Middle Ages	550–750	650	female	horse	Noyon - Orroire	France	49.571	3.018	Fages et al. 2019	32.4%	
Nustar_5	CGG_1_020439	Middle Ages	1120	1120	male	horse	Nuštar	Croatia	45.333	18.841	Fages et al. 2019	73.9%	x
Nustar_4	CGG_1_020438	Middle Ages	1120	1120	male	horse	Nuštar	Croatia	45.333	18.841	Fages et al. 2019	75.8%	x
Oktyabrsky_Rus37	CGG_1_019185	Middle Ages	763	763	male	horse	Oktyabrsky	Russia	47.967	43.644	Fages et al. 2019	31.5%	x
Oktyabrsky_Rus38	CGG_1_019186	Middle Ages	592	592	male	horse	Oktyabrsky	Russia	47.967	43.644	Fages et al. 2019	46.0%	x
OlonKurinGol_OKG1	CGG_1_018397	Iron Age	2300	2300	male	horse	Olon Kurin Gol	Mongolia	49.329	88.349	Fages et al. 2019	8.90%	x
OlonKurinGol_OKG2	CGG_1_018398	Iron Age	2300	2300	male	horse	Olon Kurin Gol	Mongolia	49.329	88.349	Fages et al. 2019	39.0%	x
Otepaa_Ote2	CGG_1_018473	Middle Ages	1117	1117	male	horse	Otepää	Estonia	58.058	26.495	Fages et al. 2019	15.8%	
Otok_OTOK16	CGG_1_020441	Middle Ages	1241	1241	female	horse	Otok	Kazakhstan	45.146	18.884	Fages et al. 2019	73.9%	x
Potapovka1_1	CGG_1_018337	Bronze Age	3690–3975	3833	female	horse	Potapovka I	Russia	53.663	50.671	Fages et al. 2019	59.2%	x
Quoygrew_VHR017	CGG_1_020952	Middle Ages	950–1150	1050	male	horse	Quoygrew	United Kingdom	59.337	–2.97	Fages et al. 2019	74.9%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Ridala_Rid1	CGG_1_018468	Bronze Age	2550–2750	2650	male	horse	Ridala	Estonia	58.455	23.033	Gaunitz et al. 2018	45.0%	
Ridala_Rid2	CGG_1_018469	Bronze Age	2550–2750	2650	male	horse	Ridala	Estonia	58.455	23.033	Fages et al. 2019	46.7%	
Saadjarve_Soa1	CGG_1_018474	Middle Ages	1050	1050	male	horse	Saadjarve	Estonia	58.543	26.678	Fages et al. 2019	50.0%	
Sagzabad_SAGS27	CGG_1_019559	Bronze Age	3050	3050	male	horse	Sagzabad	Iran	35.773	49.938	Fages et al. 2019	30.9%	
SaintJust_GVA242	CGG_1_019816	Iron Age	2183	2183	male	horse	Saint-Just-en-Chaussée	France	49.505	2.435	Fages et al. 2019	69.9%	
SaintQuentin_GVA237	CGG_1_019877	Roman period	1750–1950	1850	male	horse	Saint-Quentin	France	49.848	3.29	Fages et al. 2019	33.8%	
Sayangorsk_Rus41	CGG_1_019189	Iron Age	2610	2610	female	horse	Sayangorsk	Russia	53.097	91.416	Fages et al. 2019	51.0%	
Schloßvippach_Svi6	CGG_1_018375	Bronze Age	3550–4150	3850	male	horse	Schloßvippach	Germany	51.104	11.145	Fages et al. 2019	0.91%	
Sebastovce_131	CGG_1_018487	Middle Ages	1150–1350	1250	male	horse	Šebastovce	Slovakia	48.655	21.268	Fages et al. 2019	7.29%	
ShariQumis_AM115	CGG_1_018579	Sassanid period	1490	1490	male	horse	Shari-Qumis	Iran	35.962	54.038	Fages et al. 2019	67.5%	
ShariQumis_AM181	CGG_1_018580	Sassanid period	1627	1627	male	horse	Shari-Qumis	Iran	35.962	54.038	Gaunitz et al. 2018	71.9%	
Sintashta_NB44	CGG_1_017036	Bronze Age	3781–3978	3880	male	horse	Sintashta	Russia	55.164	61.437	Fages et al. 2019	5.84%	x
Sintashta_NB45	CGG_1_017037	Bronze Age	3781–3978	3880	male	horse	Sintashta	Russia	55.164	61.437	Fages et al. 2019	19.8%	x
Sintashta_NB46	CGG_1_017038	Bronze Age	3956	3956	female	horse	Sintashta	Russia	55.164	61.437	Librado et al. 2017	28.7%	x
SolothurnVigier_NB175	CGG_1_020499	Roman period	1650–1850	1750	male	horse	Solothurn-Vigier	Switzerland	47.233	7.517	Fages et al. 2019	11.4%	
SolothurnVigier_NB63	CGG_1_020512	Roman period	1650–1950	1800	female	horse	Solothurn-Vigier	Switzerland	47.233	7.517	Fages et al. 2019	22.3%	
Charregass_NBXRa849	CGG_1_020509	Iron Age	1550–1650	1600	male	horse	Stein am Rhein Charregass	Switzerland	47.65	8.85	Fages et al. 2019	16.3%	
SyrgalSyr11tc4	CGG_1_018920	Iron Age	2150–2350	2250	male	horse	Syrgal I	Mongolia	48.583	88.394	Fages et al. 2019	12.0%	x
SyrgalSyr11tc3	CGG_1_018919	Iron Age	2250	2250	male	horse	Syrgal I	Mongolia	48.583	88.394	Gaunitz et al. 2018	61.7%	x
TachtiPerda_TP4	CGG_1_018394	Bronze Age	3537	3537	male	horse	Tachti Perda	Georgia	41.467	46.017	Gaunitz et al. 2018	21.3%	
TavanTolgoi_GEP14	CGG_1_018050	Middle Ages	663	663	male	horse	Tavan Tolgoi	Mongolia	45.1	112.72	Fages et al. 2019	42.2%	x
TavanTolgoi_GEP13	CGG_1_018049	Middle Ages	663	663	male	horse	Tavan Tolgoi	Mongolia	45.1	112.72	Fages et al. 2019	60.3%	x
TavanTolgoi_GEP21	CGG_1_018057	Middle Ages	663	663	male	horse	Tavan Tolgoi	Mongolia	45.1	112.72	Fages et al. 2019	77.2%	x
Taymyr_CGG10029	CGG10029	Upper Palaeolithic	N/A	N/A	female	horse	Taymyr	Russia	73.046	109.708	Oriando et al. 2013	0.58%	
Taymyr_CGG10036	CGG10036	Upper Palaeolithic	N/A	N/A	male	horse	Taymyr	Russia	73.046	109.708	Oriando et al. 2013	1.25%	
Taymyr_CGG10032	CGG10032	Upper Palaeolithic	N/A	N/A	female	horse	Taymyr	Russia	73.046	109.708	Oriando et al. 2013	1.41%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Taymyr_CGG10035	CGG10035	Upper Palaeolithic	N/A	N/A	female	horse	Taymyr	Russia	73.046	109.708	Orlando et al. 2013	1.51%	
Taymyr_CGG10034	CGG10034	Upper Palaeolithic	N/A	N/A	female	horse	Taymyr	Russia	73.046	109.708	Orlando et al. 2013	1.86%	
Taymyr_CGG10023	CGG_1_010023	Upper Palaeolithic	15,989	15,989	male	horse	Taymyr	Russia	73.046	109.708	Schubert et al., 2014b	2.95%	
Taymyr_CGG10027	CGG10027	Upper Palaeolithic	N/A	N/A	female	horse	Taymyr	Russia	73.046	109.708	Orlando et al. 2013	4.16%	
Taymyr_CGG10026	CGG10026	Upper Palaeolithic	N/A	N/A	female	horse	Taymyr	Russia	73.046	109.708	Orlando et al. 2013	16.2%	
Taymyr_CGG10031	CGG10031	Upper Palaeolithic	N/A	N/A	male	horse	Taymyr	Russia	73.046	109.708	Orlando et al. 2013	19.5%	
Taymyr_CGG10022	CGG_1_010022	Upper Palaeolithic	42,691	42,691	female	horse	Taymyr	Russia	73.046	109.708	Schubert et al., 2014b	62.8%	
TepeHasanlu_2689	CGG_1_019996	Iron Age	2350–2220	2285	female	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	5.69%	
TepeHasanlu_2529	CGG_1_019988	Iron Age	2350–2220	2285	female	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	13.2%	
TepeHasanlu_3398	CGG_1_019986	Iron Age	2350–2220	2285	female	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	18.3%	
TepeHasanlu_2327	CGG_1_019995	Iron Age	2350–2220	2285	male	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	20.4%	
TepeHasanlu_1140	CGG_1_019998	Iron Age	2615	2615	female	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	30.2%	
TepeHasanlu_368	CGG_1_019994	Iron Age	2829	2829	male	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	32.6%	
TepeHasanlu_2405	CGG_1_019992	Iron Age	2819	2819	male	horse	Tepe Hasanlu	Iran	37.004	45.459	Gaunitz et al. 2018	45.3%	
TepeHasanlu_3394	CGG_1_019997	Iron Age	2741	2741	male	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	45.3%	
TepeHasanlu_3461	CGG_1_020003	Iron Age	2863	2863	female	horse	Tepe Hasanlu	Iran	37.004	45.459	Fages et al. 2019	63.6%	
TepeMehrali_Iran1	CGG_1_017447	Copper Age	5000–8000	6500	female	horse	Tepe Mehr Ali	Iran	30.678	52.162	Schubert et al. 2017	0.07%	
TepeMehrali_Iran3	CGG_1_017449	Copper Age	5000–8000	6500	male	horse	Tepe Mehr Ali	Iran	30.678	52.162	Schubert et al. 2017	0.41%	
TrouMagritte_Vert288	CGG_1_018517	Upper Palaeolithic	N/A	N/A	male	horse	Trou Magritte	Belgium	50.2231	4.913	this study	0.03%	
TrouMagritte_Vert289	CGG_1_018518	Upper Palaeolithic	N/A	N/A	male	horse	Trou Magritte	Belgium	50.2231	4.913	this study	0.06%	
TrouMagritte_Vert291	CGG_1_018520	Upper Palaeolithic	N/A	N/A	female	horse	Trou Magritte	Belgium	50.2231	4.913	this study	0.62%	
TrouMagritte_Vert331	CGG_1_018560	Upper Palaeolithic	N/A	N/A	female	horse	Trou Magritte	Belgium	50.2231	4.913	this study	1.06%	
TrouMagritte_Vert332	CGG_1_018561	Upper Palaeolithic	N/A	N/A	female	horse	Trou Magritte	Belgium	50.2231	4.913	this study	5.11%	
Uppsala_Upps02	CGG_1_018490	Palaeolithic Middle Ages	1150–1350	1250	male	horse	Uppsala	Sweden	59.861	17.639	Fages et al. 2019	16.1%	
UushgiinUvur_Mon79	CGG_1_018115	Bronze Age	2972–3063	3018	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	64.8%	x
UushgiinUvur_Mon43	CGG_1_018079	Bronze Age	3053	3053	female	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	65.3%	x

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
UushgiinUvur_Mon41	CGG_1_018077	Bronze Age	2972–3063	3018	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	66.4%	x
UushgiinUvur_Mon39	CGG_1_018075	Bronze Age	2972–3063	3018	female	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	66.6%	x
UushgiinUvur_Mon44	CGG_1_018080	Bronze Age	2972–3063	3018	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	68.5%	x
UushgiinUvur_Mon40	CGG_1_018076	Bronze Age	2972–3063	3018	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	69.0%	x
UushgiinUvur_Mon89	CGG_1_018125	Bronze Age	2972–3063	3018	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	69.5%	x
UushgiinUvur_Mon87	CGG_1_018123	Bronze Age	3050	3050	female	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	70.7%	x
UushgiinUvur_Mon84	CGG_1_018120	Bronze Age	3056	3056	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Gaunitz et al. 2018	72.3%	x
UushgiinUvur_Mon86	CGG_1_018122	Bronze Age	2972	2972	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Gaunitz et al. 2018	72.9%	x
UushgiinUvur_Mon45	CGG_1_018081	Bronze Age	3013	3013	female	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	73.2%	x
UushgiinUvur_Mon37	CGG_1_018073	Bronze Age	2972–3063	3018	male	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	74.0%	x
UushgiinUvur_Mon42	CGG_1_018078	Bronze Age	3063	3063	female	horse	Uushgiin Uvur	Mongolia	49.656	99.912	Fages et al. 2019	74.4%	x
Vermand_GVA199	CGG_1_019773	Roman period	1650–1700	1675	female	horse	Vermand, rue De Gaulle	France	49.877	3.146	Fages et al. 2019	71.0%	x
Vicerrectorado_VIR175	CGG_1_016987	Roman period	1550–1750	1650	male	horse	Vicerrectorado	Spain	43.009	– 7.559	Fages et al. 2019	11.2%	
WhitehallRomanVilla_UK08	CGG_1_019435	Roman period	1550–1650	1600	male	horse	Whitehall Roman Villa	United Kingdom	52.226	– 1.057	Fages et al. 2019	37.0%	
WitterPlace_UK18	CGG_1_019445	Early Modern period	150–250	200	female	horse	Witter Place	United Kingdom	53.193	– 2.883	Fages et al. 2019	76.5%	
WitterPlace_UK19	CGG_1_019446	Early Modern period	150–250	200	male	horse	Witter Place	United Kingdom	53.193	– 2.883	Fages et al. 2019	77.7%	
WitterPlace_UK17	CGG_1_019444	Early Modern period	150–250	200	female	horse	Witter Place	United Kingdom	53.193	– 2.883	Fages et al. 2019	78.0%	
Yenikapi_Tur171	CGG_1_018737	Byzantine period	1622	1622	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	67.0%	
Yenikapi_Tur175	CGG_1_018741	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	69.6%	
Yenikapi_Tur172	CGG_1_018738	Byzantine period	1628	1628	male	horse	Yenikapi	Turkey	41.005	28.952	Gaunitz et al. 2018	71.9%	
Yenikapi_Tur229	CGG_1_018795	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	71.9%	
Yenikapi_Tur194	CGG_1_018760	Byzantine period	1293	1293	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	72.3%	
Yenikapi_Tur193	CGG_1_018759	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	73.1%	
Yenikapi_Tur170	CGG_1_018736	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	73.2%	
Yenikapi_Tur145	CGG_1_018711	Byzantine period	1089	1089	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	73.6%	
Yenikapi_Tur150	CGG_1_018716	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	73.9%	

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Table A1 (continued)

Sample	Registration number	Period	Age range (years cal BP)	Age mean (years cal BP)	Sex	Species	Site	Country	Latitude	Longitude	Publication	Endogenous fraction	Funerary context
Yenikapi_Tur142	CGG_1_018708	Byzantine period	1329	1329	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	74.2%	
Yenikapi_Tur243	CGG_1_018809	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	74.5%	
Yenikapi_Tur173	CGG_1_018739	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	74.7%	
Yenikapi_Tur176	CGG_1_018742	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	74.7%	
Yenikapi_Tur146	CGG_1_018712	Byzantine period	1663	1663	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	74.8%	
Yenikapi_Tur140	CGG_1_018706	Byzantine period	1222	1222	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	74.9%	
Yenikapi_Tur141	CGG_1_018707	Byzantine period	1363	1363	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	76.0%	
Yenikapi_Tur181	CGG_1_018747	Byzantine period	1089–1663	1376	male	horse	Yenikapi	Turkey	41.005	28.952	Fages et al. 2019	76.0%	
Yerqorqan_YER28	CGG_1_020254	Iron Age	2786	2786	male	horse	Yerqorqan	Uzbekistan	38.867	65.8	Fages et al. 2019	26.7%	
Zhanaturmus_Issyk1	CGG_1_018577	Middle Ages	1076	1076	male	horse	Zhanaturmus	Kazakhstan	43.184	76.78	Gaunitz et al. 2018	77.9%	x

Table B1

Statistical performance of molecular sex assignment for females. Those tests showing a true-positive rate superior or equal to 95% are highlighted in bold fonts.

#Reads	Sex	#Females assigned	#Males assigned	#No assignment
100	F	61	24	15
200	F	72	18	10
300	F	79	16	5
400	F	79	16	5
500	F	84	13	3
600	F	92	5	3
700	F	90	7	3
800	F	91	7	2
900	F	95	5	0
1000	F	97	2	1
1100	F	95	4	1
1200	F	92	6	2
1300	F	100	0	0
1400	F	97	3	0
1500	F	97	1	2
1600	F	98	2	0
1700	F	98	2	0
1800	F	100	0	0
1900	F	99	1	0
2000	F	100	0	0
3000	F	100	0	0
4000	F	100	0	0
5000	F	100	0	0

Table C1

Statistical performance of molecular sex assignment for males. Those tests showing a true-positive rate superior or equal to 95% are highlighted in bold fonts.

#Reads	Sex	#Females assigned	#Males assigned	#No assignment
100	M	13	69	15
200	M	9	85	6
300	M	3	94	3
400	M	4	94	2
500	M	4	93	3
600	M	2	98	0
700	M	6	93	1
800	M	2	97	1
900	M	2	98	0
1000	M	2	97	1
1100	M	1	99	0
1200	M	2	98	0
1300	M	0	100	0
1400	M	1	99	0
1500	M	0	100	0
1600	M	1	99	0
1700	M	0	100	0
1800	M	0	100	0
1900	M	0	100	0
2000	M	1	99	0
3000	M	0	100	0
4000	M	0	100	0
5000	M	0	100	0

References

- Anthony, D.W., 2007. The Wheel, the Horse, and Language.
- Anthony, D.W., Brown, D.R., 2011. The secondary products revolution, horse-riding, and mounted warfare. *J. World Prehist.* 24, 131.
- Baxter, I.L., 1998. Species identification of equids from Western European archaeological deposits: methodologies, techniques and problems. In: *Current and Recent Research in Osteoarchaeology*, Proceedings of the Third Meeting of the Osteoarchaeology Research Group. Oxbow, Oxford. pp. 3–17.
- Benecke, N., von den Driesch, A., 2003. Horse exploitation in the Kazakh steppes during the Eneolithic and Bronze Age. *Prehistoric steppe adaptation and the horse*, 69–82.
- Bertašius, M., Daugnora, L., 2001. Viking age horse graves from Kaunas region (Middle Lithuania). *Int. J. Osteoarchaeol.* 11, 387–399.
- Briggs, A.W., Stenzel, U., Johnson, P.L.F., Green, R.E., Kelso, J., Prüfer, K., Meyer, M., Krause, J., Ronan, M.T., Lachmann, M., Pääbo, S., 2007. Patterns of damage in genomic DNA sequences from a Neandertal. *Proc. Natl. Acad. Sci. USA* 104, 14616–14621.
- Der Sarkissian, C., Ermini, L., Schubert, M., Yang, M.A., Librado, P., Fumagalli, M., Jónsson, H., Bar-Gal, G.K., Albrechtsen, A., VieiraOthers, F.G., 2015. Evolutionary genomics and conservation of the endangered Przewalski's horse. *Curr. Biol.* 25, 2577–2583.
- Drews, R., 2004. *Early Riders: The Beginnings of Mounted Warfare in Asia and Europe*. Routledge.
- Fages, A., Hanghøj, K., Khan, N., Gaunitz, C., Seguin-Orlando, A., Leonardi, M., McGroarty Constantz, C., Gamba, C., Al-Rasheid, K.A.S., Albizuri, S., Alfarhan, A.H., Allentoft, M., Alquraishi, S., Anthony, D., Baimukhanov, N., Barrett, J.H., Bayarsaikhan, J., Benecke, N., Bernáldez-Sánchez, E., Berrocal-Rangel, L., Biglari, F., Boessenkool, S., Boldgiv, B., Brem, G., Brown, D., Burger, J., Crubézy, E., Daugnora, L., Davoudi, H., de Barros Damgaard, P., Los Angeles de Chorro Y de Villa-Ceballos, M., Deschler-Erb, S., Detry, C., Dill, N., do Mar Oom, M., Dohr, A., Ellingvåg, S., Erdenebaatar, D., Fathi, H., Felkel, S., Fernández-Rodríguez, C., García-Viñas, E., Germonpré, M., Granado, J.D., Hallsson, J.H., Hemmer, H., Hofreiter, M., Kasparov, A., Khasanov, M., Khazaeli, R., Kosintsev, P., Kristiansen, K., Kubatbek, T., Kuderna, L., Kuznetsov, P., Laleh, H., Leonard, J.A., Lhuillier, J., Liesau von Lettow-Vorbeck, C., Logvin, A., Lõugas, L., Ludwig, A., Luis, C., Arruda, A.M., Marques-Bonet, T., Matoso Silva, R., Merz, V., Mijidorj, E., Miller, B.K., Monchalov, O., Mohaseb, F.A., Morales, A., Nieto-Espineta, A., Nistelberger, H., Onar, V., Pálsdóttir, A.H., Pitulko, V., Pitskhelauri, K., Pruvost, M., Rajic Sikanjic, P., Rapan Papeša, A., Roslyakova, N., Sardari, A., Sauer, E., Schafberg, R., Scheu, A., Schibler, J., Schlumbaum, A., Serrand,

- N., Serres-Armero, A., Shapiro, B., Sheikhi Seno, S., Shevnina, I., Shidrang, S., Southon, J., Star, B., Sykes, N., Taheri, K., Taylor, W., Teegen, W.-R., Trbojević Vukičević, T., Trixl, S., Tumen, D., Undrakhbold, S., Usmanova, E., Vahdati, A., Valenzuela-Lamas, S., Viegas, C., Wallner, B., Weinstock, J., Zaubert, V., Clavel, B., Lepetz, S., Mashkour, M., Helgason, A., Stefánsson, K., Barrey, E., Willerslev, E., Outram, A.K., Librado, P., Orlando, L., 2019. Tracking five millennia of horse management with extensive ancient genome time series. *Cell* 177, 1419–1435.e31.
- Felkel, S., Vogl, C., Rigler, D., Jagannathan, V., Leeb, T., Fries, R., Neuditschko, M., Rieder, S., Velie, B., Lindgren, G., Rubin, C.-J., Schlotterer, C., Rattei, T., Brem, G., Wallner, B., 2018. Asian horses deepen the MSY phylogeny. *Anim. Genet.* 49, 90–93.
- Frie, A.C., 2018. Horses and the embodiment of elite masculinity in the dolnjska hallstatt culture. *Oxford J. Archaeol.*
- Gamba, C., Hanghøj, K., Gaunitz, C., Alfarhan, A.H., Alquraishi, S.A., Al-Rasheid, K.A.S., Bradley, D.G., Orlando, L., 2016. Comparing the performance of three ancient DNA extraction methods for high-throughput sequencing. *Mol. Ecol. Resour.* 16, 459–469.
- Gaunitz, C., Fages, A., Hanghøj, K., Albrechtsen, A., Khan, N., Schubert, M., Seguin-Orlando, A., Owens, I.J., Felkel, S., Bignon-Lau, O., de Barros Damgaard, P., 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., Zaubert, 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.
- Germonpré, M., 1997. The Magdalenian upper horizon of Goyet and the late Upper Palaeolithic recolonisation of the Belgian Ardennes. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Série Sciences de la Terre* 67, 167–182.
- Gower, G., Fenderson, L.E., Salis, A.T., Helgen, K.M., van Loenen, A.L., Heiniger, H., Hofman-Kamińska, E., Kowalczyk, R., Mitchell, K.J., Llamas, B., Cooper, A., 2019. Widespread male sex bias in mammal fossil and museum collections. *Proc. Natl. Acad. Sci. USA* 116, 19019–19024.
- Jacobson-Tepfer, E., 2012. The image of the wheeled vehicle in the Mongolian Altai: instability and ambiguity. *Silk Road* 10, 1–28.
- Jones-Bley, K., 2000. The Sintashta "Chariots." Kurgans, ritual sites, and settlements: Eurasian Bronze and Iron Age, 135–140.
- Kelekna, P., 2009. *The Horse in Human History*. Cambridge University Press, Cambridge.
- Kosintsev, P., 2010. The harness horse phenomenon. *Horses, Chariots, and Chariot Drivers of the Eurasian Steppes*, 257–291.
- Kosintsev, P., Kuznetsov, P., 2013. Comment on "The Earliest Horse Harnessing and Milking." *Tyragetia. Serie nouă* 405–408.
- Kristiansen, K., Rowlands, M., 2005. *Social Transformations in Archaeology: Global and Local Perspectives*. Routledge.
- Larson, G., Fuller, D.Q., 2014. The evolution of animal domestication. *Annu. Rev. Ecol. Evol. Syst.* 45, 115–136.
- Lepetz, S., 2013. Horse Sacrifice in a Pazyryk Culture Kurgan: The Princely Tomb of Berel' (Kazakhstan). *Selection Criteria and Slaughter Procedures. Anthropolozoolgia*.
- Levine, M.A., 1999. Botai and the origins of horse domestication. *J. Anthropol. Archaeol.* 18, 29–78.
- Librado, P., Der Sarkissian, C., Ermini, L., Schubert, M., Jónsson, H., Albrechtsen, A., Fumagalli, M., Yang, M.A., Gamba, C., Seguin-Orlando, A., Mortensen, C.D., Petersen, B., Hoover, C.A., Lorente-Galdos, B., Nedoluzhko, A., Boulygina, E., Tsygankova, S., Neuditschko, M., Jagannathan, V., Thèves, C., Alfarhan, A.H., Alquraishi, S.A., Al-Rasheid, K.A.S., Sicheritz-Ponten, T., Popov, R., Grigoriev, S., Alekseev, A.N., Rubin, E.M., McCue, M., Rieder, S., Leeb, T., Tikhonov, A., Crubézy, E., Slatkin, M., Marques-Bonet, T., Nielsen, R., Willerslev, E., Kantanen, J., Prokhortchouk, E., Orlando, L., 2015. Tracking the origins of Yakutian horses and the genetic basis for their fast adaptation to subarctic environments. *Proc. Natl. Acad. Sci. USA* 112, E6889–E6897.
- Librado, P., Gamba, C., Gaunitz, C., Der Sarkissian, C., Pruvost, M., Albrechtsen, A., Fages, A., Khan, N., Schubert, M., Jagannathan, V., Serres-Armero, A., Kuderna, L.F.K., Povolotskaya, I.S., Seguin-Orlando, A., Lepetz, S., Neuditschko, M., Thèves, C., Alquraishi, S., Alfarhan, A.H., Al-Rasheid, K., Rieder, S., Samashev, Z., Francfort, H.-P., Benecke, N., Hofreiter, M., Ludwig, A., Keyser, C., Marques-Bonet, T., Ludes, B., Crubézy, E., Leeb, T., Willerslev, E., Orlando, L., 2017. Ancient genomic changes associated with domestication of the horse. *Science* 356, 442–445.
- Li, H., Durbin, R., 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics*.
- Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., 1000 Genome Project Data Processing Subgroup, 2009. The sequence alignment/Map format and SAMtools. *Bioinformatics* 25, 2078–2079.
- McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernysky, A., Garimella, K., Altshuler, D., Gabriel, S., Daly, M., DePristo, M.A., 2010. The genome analysis toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res.* 20, 1297–1303.
- Meyer, M., Kircher, M., 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb. Protoc.* 2010, db.prot5448.
- Nistelberger, H.M., Pálsdóttir, A.H., Star, B., Leifsson, R., Gondek, A.T., Orlando, L., Barrett, J.H., Hallsson, J.H., Boessenkool, S., 2019. Sexing Viking Age horses from burial and non-burial sites in Iceland using ancient DNA. *J. Archaeol. Sci.* 101, 115–122.
- Novozhenov, V.A., Rogozhonskiy, A.E., 2019. New themes of chariots in petroglyphs in Valley of Koksuy River (Eshkiolmes). *History Archaeol. Semirechye* 6, 170–196.
- Olsen, S., Bradley, B., Maki, D., Outram, A., 2006. Community organisation among Copper Age sedentary horse pastoralists of Kazakhstan. In: *Beyond the Steppe and the Sown: Proceedings of the 2002 University of Chicago Conference on Eurasian Archaeology*. pp. 89–111.
- Olsen, S.L., 2006. Early horse domestication: weighing the evidence. *BAR Int. Ser.* 1560, 81.
- Orlando, Ludovic, 2020. Ancient genomes reveal unexpected horse domestication and management dynamics. *BioEssays* 42 (1), 1900164. <https://doi.org/10.1002/bies.v42.110.1002/bies.201900164>.
- Orlando, L., Ginolhac, A., Zhang, G., Froese, D., Albrechtsen, A., Stiller, M., Schubert, M., Cappellini, E., Petersen, B., Moltke, I., Johnson, P.L.F., Fumagalli, M., Vilstrup, J.T., Raghavan, M., Korneliusen, T., Malaspina, A.-S., Vogt, J., Szklarczyk, D., Kelstrup, C.D., Vinther, J., Dolocan, A., Stenderup, J., Velazquez, A.M.V., Cahill, J., Rasmussen, M., Wang, X., Min, J., Zazula, G.D., Seguin-Orlando, A., Mortensen, C., Magnussen, K., Thompson, J.F., Weinstock, J., Gregersen, K., Røed, K.H., Eisenmann, V., Rubin, C.J., Miller, D.C., Antczak, D.F., Bertelsen, M.F., Brunak, S., Al-Rasheid, K.A.S., Ryder, O., Andersson, L., Mundy, J., Krogh, A., Gilbert, M.T.P., Kjær, K., Sicheritz-Ponten, T., Jensen, L.J., Olsen, J.V., Hofreiter, M., Nielsen, R., Shapiro, B., Wang, J., Willerslev, E., 2013. Recalibrating Equus evolution using the genome sequence of an early Middle Pleistocene horse. *Nature* 499, 74–78.
- Otte, M., Straus, L.-G., 1996. Le Trou Magritte. *Fouilles 1991–1992. Bulletin-société préhistorique française* 93, 455.
- Outram, A.K., Stear, N.A., Bendrey, R., Olsen, S., Kasparov, A., Zaubert, V., Thorpe, N., Evershed, R.P., 2009. The earliest horse harnessing and milking. *Science* 323, 1332–1335.
- Pečnerová, P., Diez-Del-Molino, D., Dussex, N., Feuerborn, T., von Seth, J., van der Plicht, J., Nikolskiy, P., Tikhonov, A., Vartanyan, S., Dalén, L., 2017. Genome-based sexing provides clues about behavior and social structure in the Woolly Mammoth. *Curr. Biol.* 27, 3505–3510.e3.
- Core Team, R., 2013. R development core team. *RA Lang. Environ. Stat. Comput.* 55, 275–286.
- Robb, J., Harris, O.J.T., 2018. Becoming gendered in European prehistory: was neolithic gender fundamentally different? *Am. Antiq.* 83, 128–147.
- Schubert, M., Ermini, L., Der Sarkissian, C., Jónsson, H., Ginolhac, A., Schaefer, R., Martin, M.D., Fernández, R., Kircher, M., McCue, M., Willerslev, E., Orlando, L., 2014a. Characterization of ancient and modern genomes by SNP detection and phylogenomic and metagenomic analysis using PALEOMIX. *Nat. Protoc.* 9, 1056–1082.
- Schubert, M., Jónsson, H., Chang, D., Der Sarkissian, C., Ermini, L., Ginolhac, A., Albrechtsen, A., Dupanloup, I., Foucal, A., Petersen, B., Fumagalli, M., Raghavan, M., Seguin-Orlando, A., Korneliusen, T.S., Velazquez, A.M.V., Stenderup, J., Hoover, C.A., Rubin, C.-J., Alfarhan, A.H., Alquraishi, S.A., Al-Rasheid, K.A.S., MacHugh, D.E., Kalbfleisch, T., MacLeod, J.N., Rubin, E.M., Sicheritz-Ponten, T., Andersson, L., Hofreiter, M., Marques-Bonet, T., Gilbert, M.T.P., Nielsen, R., Excoffier, L., Willerslev, E., Shapiro, B., Orlando, L., 2014b. Prehistoric genomes reveal the genetic foundation and cost of horse domestication. *Proc. Natl. Acad. Sci. USA* 111, E5661–E5669.
- Schubert, M., Lindgreen, S., Orlando, L., 2016. AdapterRemoval v2: rapid adapter trimming, identification, and read merging. *BMC Res. Notes* 9, 88.
- Schubert, M., Mashkour, M., Gaunitz, C., Fages, A., Seguin-Orlando, A., Sheikhi, S., Alfarhan, A.H., Alquraishi, S.A., Al-Rasheid, K.A.S., Chuang, R., Ermini, L., Gamba, C., Weinstock, J., Vedat, O., Orlando, L., 2017. Zonkey: a simple, accurate and sensitive pipeline to genetically identify equine F1-hybrids in archaeological assemblages. *J. Archaeol. Sci.* 78, 147–157.
- Taylor, W., 2017. Horse demography and use in Bronze Age Mongolia. *Quat. Int.* 436, 270–282.
- Wade, C.M., Giulotto, E., Sigurdsson, S., Zoli, M., Gnerre, S., Inslund, F., Lear, T.L., Adelson, D.L., Bailey, E., Bellone, R.R., Blöcker, H., Distl, O., Edgar, R.C., Garber, M., Leeb, T., Mauceli, E., MacLeod, J.N., Penedo, M.C.T., Raison, J.M., Sharpe, T., Vogel, J., Andersson, L., Antczak, D.F., Biagi, T., Binns, M.M., Chowdhary, B.P., Coleman, S.J., Della Valle, G., Fryc, S., Guérin, G., Hasegawa, T., Hill, E.W., Jurka, J., Kiialainen, A., Lindgren, G., Liu, J., Magnani, E., Mickelson, J.R., Murray, J., Nergadze, S.G., Onofrio, R., Pedroni, S., Piras, M.F., Raudsepp, T., Rocchi, M., Røed, K.H., Ryder, O.A., Searle, S., Skow, L., Swinburne, J.E., Syvänen, A.C., Tozaki, T., Valberg, S.J., Vaudin, M., White, J.R., Zody, M.C., Broad Institute Genome Sequencing Platform, Broad Institute Whole Genome Assembly Team, Lander, E.S., Lindblad-Toh, K., 2009. Genome sequence, comparative analysis, and population genetics of the domestic horse. *Science* 326, 865–867.
- Wallner, B., Palmieri, N., Vogl, C., Rigler, D., Bozjak, E., Druml, T., Jagannathan, V., Leeb, T., Fries, R., Tetens, J., Thaller, G., Metzger, J., Distl, O., Lindgren, G., Rubin, C.-J., Andersson, L., Schaefer, R., McCue, M., Neuditschko, M., Rieder, S., Schlotterer, C., Brem, G., 2017. Y chromosome uncovers the recent oriental origin of modern stallions. *Curr. Biol.* 27, 2029–2035.e5.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer.
- Wutke, S., Sandoval-Castellanos, E., Benecke, N., Döhle, H.-J., Friederich, S., Gonzalez, J., Hofreiter, M., Lõugas, L., Magnell, O., Malaspina, A.-S., Morales-Muñiz, A., Orlando, L., Reissmann, M., Trinks, A., Ludwig, A., 2018. Decline of genetic diversity in ancient domestic stallions in Europe. *Sci. Adv.* 4, eaap9691.
- Yang, G.C., Croaker, D., Zhang, A.L., Manglick, P., Cartmill, T., Cass, D., 1998. A dinucleotide mutation in the endothelin-B receptor gene is associated with lethal white foal syndrome (LWFS); a horse variant of Hirschsprung disease. *Hum. Mol. Genet.* 7, 1047–1052.
- Zeder, M.A., 2012. The domestication of animals. *J. Anthropol. Res.* 68, 161–190.