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

Antoine Fages [a,*], Andaine Seguin-Orlando [a], Mietje Germonpré [b], Ludovic Orlando [a,c]

[a] *Laboratoire d'Anthropologie Moléculaire et d'Imagerie de Synthèse CNRS UMR 5288, Université de Toulouse, Université Paul Sabatier, 31000 Toulouse, France*
[b] *Operational Direction, Earth and History of Life, Royal Belgian Institute of Natural Sciences, 1000 Brussels, Belgium*
[c] *Globe Institute, Lundbeck Foundation GeoGenetics Centre, University of Copenhagen, 1350K Copenhagen, Denmark*

| ARTICLE INFO | 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

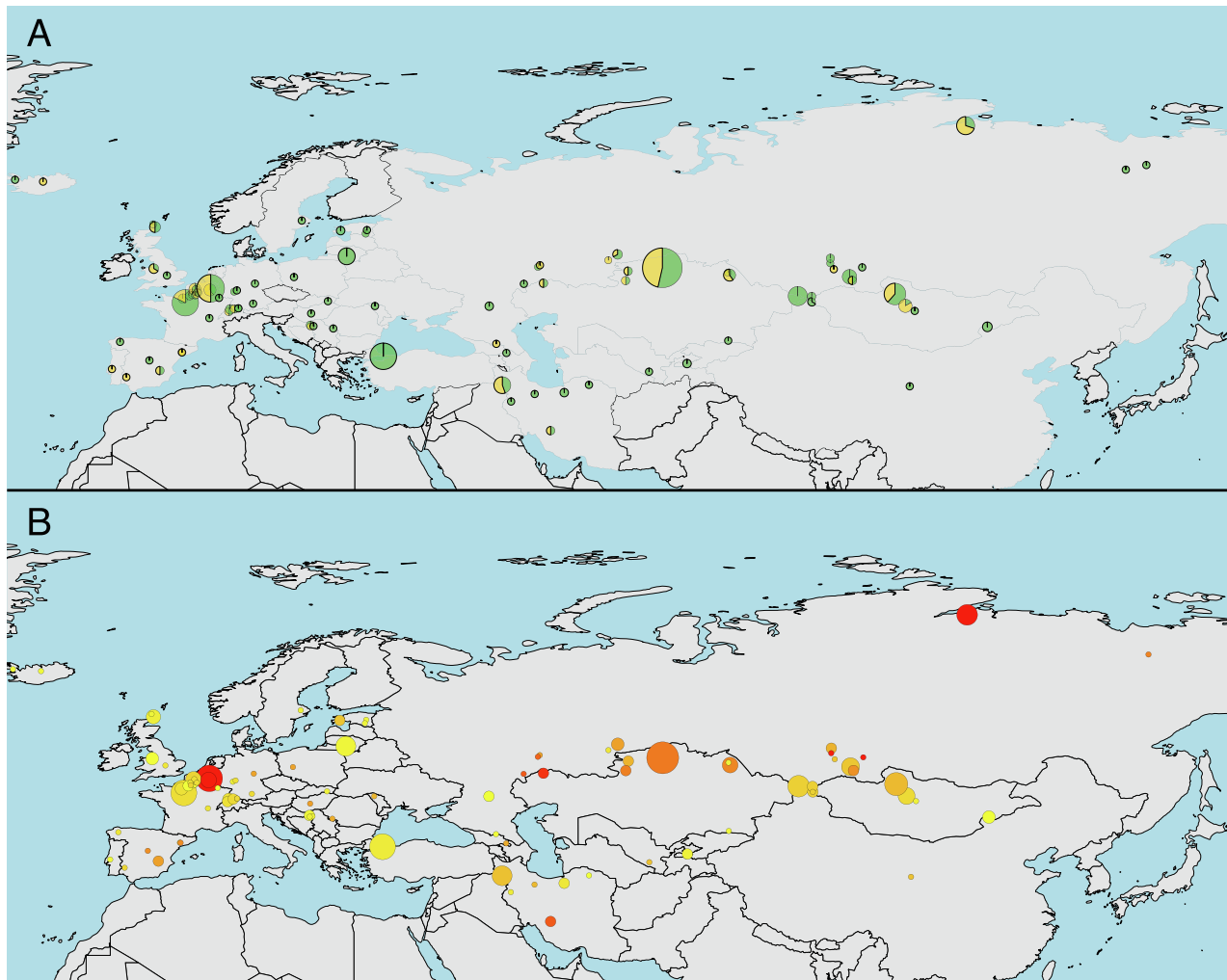**Fig. 1.** Geographical distribution of horses included in this study. A. Geographical distribution of female and male horses. Pie charts are proportional to the total number of specimens excavated at each site. Gold refers to females and green to males. B. Temporal and geographical distribution of 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.

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).

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

**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 |
| TrouMagrite_Vert288 | CGG_1_018517 | 200 | Yang et al (1998), modified by Gamba et al (2016) | 2nd | yes | Meyer and Kircher (2010) | Accuprime | 9 | ATGGTT |
| TrouMagrite_Vert289 | CGG_1_018518 | 295 | Yang et al (1998), modified by Gamba et al (2016) | 2nd | yes | Meyer and Kircher (2010) | Accuprime | 9 | ATTAAA |
| TrouMagrite_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 | GCCAAT |
| Goyet_Vert301 | CGG_1_018530 | 200 | Yang et al (1998), modified by Gamba et al (2016) | 2nd | yes | Meyer and Kircher (2010) | Accuprime | 16 | GCCAAT |
| 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 |
| TrouMagrite_Vert331 | CGG_1_018560 | 380 | Yang et al (1998), modified by Gamba et al (2016) | 2nd | yes | Meyer and Kircher (2010) | Accuprime | 10 | ATTCTC |
| TrouMagrite_Vert332 | CGG_1_018561 | 455 | Yang et al (1998), modified by Gamba et al (2016) | 2nd | yes | Meyer and Kircher (2010) | Accuprime | 9 | CAAAAT |

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$^{TM}$ 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$^{TM}$ 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

**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 |

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 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-

**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 |
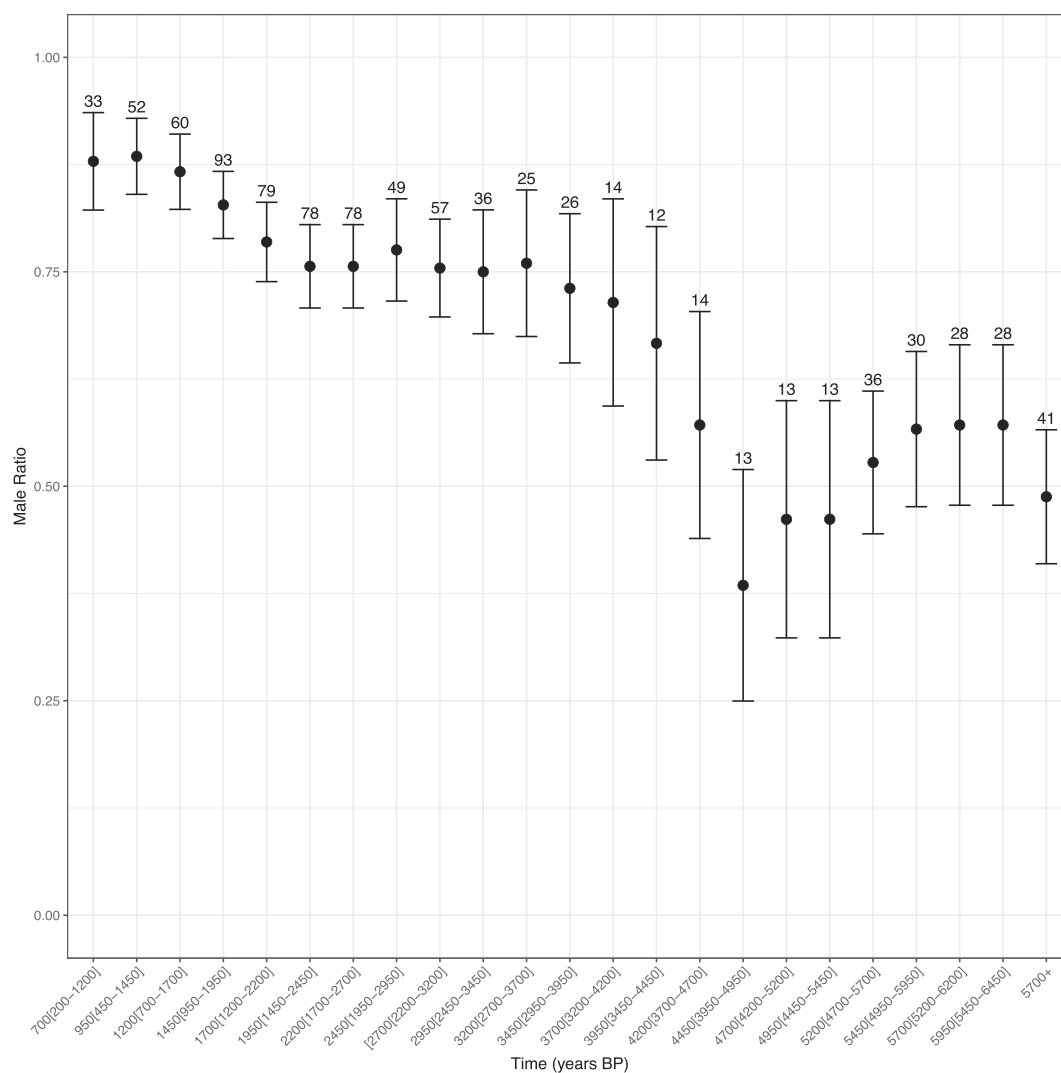


**Fig. 2.** Evolution of male ratios through time. Error bars indicate standard deviations from binomial distributions, figures above error bars indicate the number of samples in each bin.

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., 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 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 sedentary and larger villages with a subsistence model almost exclusively based on horses (Gaunitz 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 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, 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.

## Acknowledgements

## Appendices
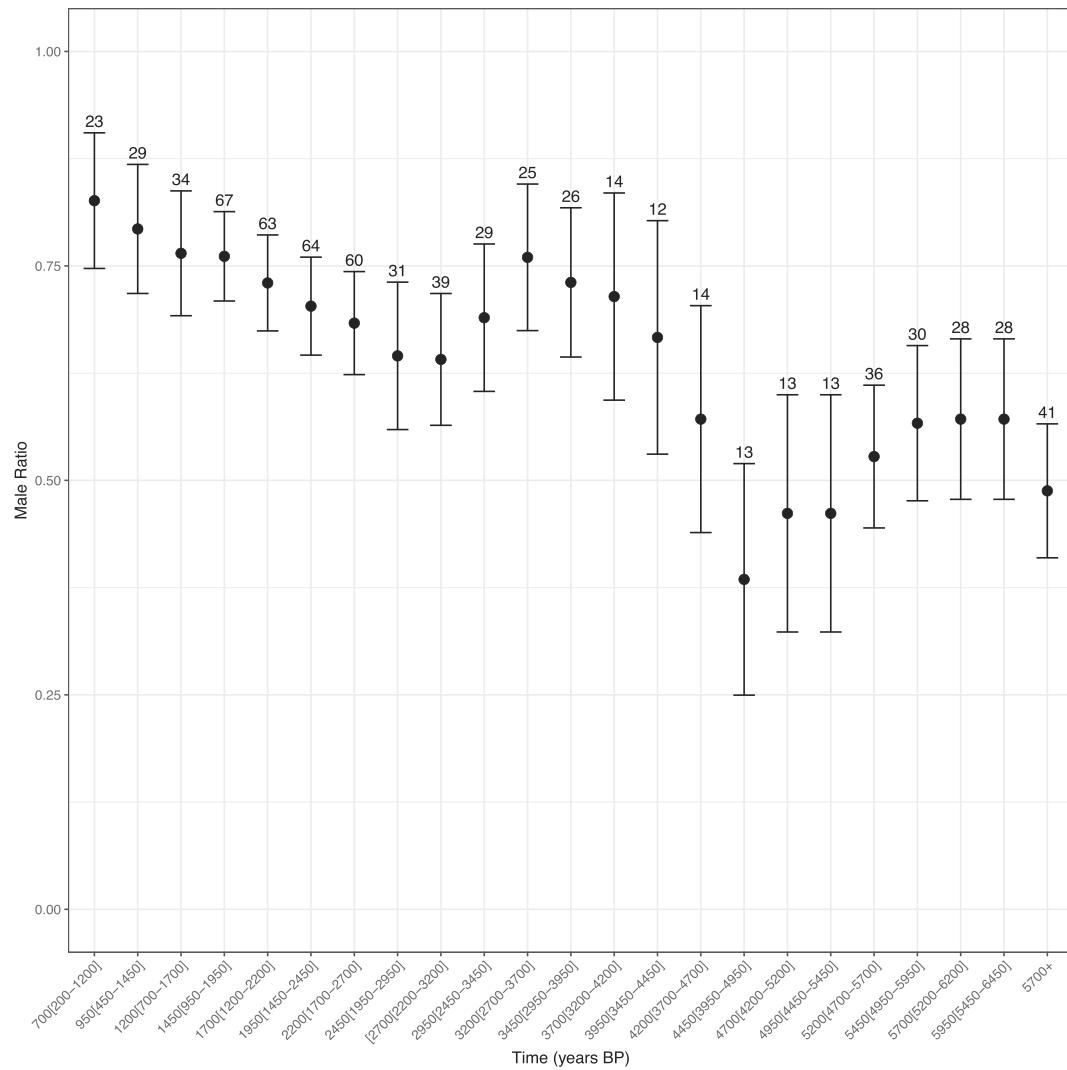
**Fig. A1.** Evolution of male ratios through time for the reduced dataset. The reduced dataset excludes sites for which at least five horses but only one sex was identified, and consists of 224 individuals. Error bars indicate standard deviations from binomial distributions, figures above error bars 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_I-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_I-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% | |
| Bateni_Rus14 | CGG_1_019164 | Bronze Age | 3251 | 3251 | male | horse | Bateni | Russia | 54.624 | 90.945 | Gaunitz et al. 2018 | 33.8% | |
| Bateni_Rus16 | CGG_1_019166 | Bronze Age | 3283 | 3283 | male | horse | Bateni | 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% | |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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% | |
| 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% | |

**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_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% | |
| 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% | |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 |
| 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 | | France | 48.442 | 1.494 | Fages et al. 2019 | 74.7% | |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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% | |
| Dangstetten_R10DA | CGG_1_017516 | Roman period | 1959–1965 | 1962 | male | horse | Dangstetten | 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 | Dunaújváros | 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_Fen4 | CGG_1_018396 | Iron Age | 2753 | 2753 | male | horse | Fengtai | China | 36.841 | 101.958 | Fages et al. 2019 | 16.3% | |
| FrankfurtHeddernheim_Fr1 | CGG_1_018151 | Roman period | 1796 | 1796 | male | horse | Frankfurt-Heddenheim | Germany | 50.161 | 8.642 | Fages et al. 2019 | 73.6% | |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fmontauban_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% | |
| 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% | |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Granastadir_VHR031 | CGG_1_020955 | Middle Ages | 850–1150 | 1000 | female | horse | Granastaðir | 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 |
| Haunstetten_1979 | CGG_1_017139 | Roman period | 1912 | 1912 | male | horse | Haunstetten | 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 |
| Khotont_UCIE2012x85 | CGG_1_018038 | Middle Ages | 1224 | 1224 | male | horse | Khotont | 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% | |
| 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 | Marvelė 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 | Marvelė 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 | Marvelė 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 | Marvelė 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 | Marvelė 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 | Marvelė cemetery | Lithuania | 54.897 | 23.872 | Fages et al. 2019 | 58.9% | x |
| Marvele_18 | CGG_1_019405 | Middle Ages | 1122 | 1122 | male | horse | Marvelė cemetery | Lithuania | 54.897 | 23.872 | Fages et al. 2019 | 72.1% | x |
| Marvele_21 | CGG_1_019408 | Middle Ages | 1020 | 1020 | male | horse | Marvelė cemetery | Lithuania | 54.897 | 23.872 | Fages et al. 2019 | 74.9% | x |
| Marvele_32 | CGG_1_019419 | Middle Ages | 1077 | 1077 | male | horse | Marvelė cemetery | Lithuania | 54.897 | 23.872 | Fages et al. 2019 | 75.0% | x |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 |
| Miciurin_Mic2 | CGG_1_018388 | Bronze Age | 2950–3450 | 3200 | male | horse | Miciurin | 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 |
| PotapovkaI_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% | |
| 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_Saa1 | CGG_1_018474 | Middle Ages | 1050 | 1050 | male | horse | Saadjärve | 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 | Shar-I-Qumis | Iran | 35.962 | 54.038 | Fages et al. 2019 | 67.5% | |
| SharIQumis_AM181 | CGG_1_018580 | Sassanid period | 1627 | 1627 | male | horse | Shar-I-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 | | 5.84% | x |

| 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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | Fages et al. 2019 | | |
| 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 | Steim am Rhein Charregass | Switzerland | 47.65 | 8.85 | Fages et al. 2019 | 16.3% | |
| Syrgal_Syr1t1c4 | CGG_1_018920 | Iron Age | 2150–2350 | 2250 | male | horse | Syrgal 1 | Mongolia | 48.583 | 88.394 | Fages et al. 2019 | 12.0% | x |
| Syrgal_Syr1t1c3 | CGG_1_018919 | Iron Age | 2250 | 2250 | male | horse | Syrgal 1 | 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 | Orlando et al. 2013 | 0.58% | |
| Taymyr_CGG10036 | CGG10036 | Upper Palaeolithic | N/A | N/A | male | horse | Taymyr | Russia | 73.046 | 109.708 | Orlando et al. 2013 | 1.25% | |
| Taymyr_CGG10032 | CGG10032 | Upper Palaeolithic | N/A | N/A | female | horse | Taymyr | Russia | 73.046 | 109.708 | Orlando et al. 2013 | 1.41% | |
| 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 | | 20.4% | |

**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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 | 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 |
| 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 | | 74.4% | x |

19

| 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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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% | |
| 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., McCrory 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 Damgaardde, P., Los Ángeles 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., Mijiddorj, E., Miller, B.K., Monchalov, O., Mohaseb, F.A., Morales, A., Nieto-Espinet, 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., Zaibert, 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., Schlötterer, 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 dolenjska 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., 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.

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 nouǎ 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. Anthropozoologica.

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., Kernytsky, 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 Koksu 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., Korneliussen, T., Malaspinas, 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 Magrite. Fouilles 1991–1992. Bulletin-société préhistorique française 93, 455.

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.

Pečnerová, P., Díez-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., Korneliussen, 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., Imsland, 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., Bozlak, 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., Schlötterer, 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., Malaspinas, 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.