









# Extended pre-domestication horse lineage survival in the Carpathian Basin

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Acta Archaeologica  
Academiae Scientiarum  
Hungaricae

76 (2025) 2, 251–262

DOI:  
[10.1556/072.2025.00036](https://doi.org/10.1556/072.2025.00036)  
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Received: February 4, 2025 • Accepted: September 18, 2025

## ORIGINAL RESEARCH PAPER



## ABSTRACT

Horse domestication is a key element in history for its impact on human mobility and warfare. There is a clear evidence for horse control from the beginning of the 2nd millennium BCE in the Carpathian Basin, when antler cheekpieces appear in the archaeological record mostly in the eastern areas. Previous archaeogenomic studies also revealed that the spread of the ancestors of modern day horses began at this time period, although the replacement dynamics is less understood in Europe. In this study we report a new shotgun genome ( $\sim 0.9\times$  average genomic coverage) of a Middle Bronze Age horse (1870–1620 cal. BCE) from Tompa site, southern Hungary. Our results reveal an extended survival of pre-domestication lineage compared to available estimates, and a strong bottleneck in prevailing non-domesticated lineages, compared to the surrounding areas, and provide additional information on human-horse interactions in this area.

## KEYWORDS

ancient DNA, population genomics, horse, paleoecology

## INTRODUCTION

The horse is one of the most impactful and versatile animals ever domesticated, which revolutionised trade, social stratification, workforce, warfare and human mobility. Still, our knowledge on the process and stages of horse domestication is incomplete. Both archaeological and genetic evidence points to the utilisation of these animals in husbandry through the findings of Botai (Kazakhstan) or Dereivka (Ukraine) sites.<sup>1</sup> Despite being managed by humans, further genetic evidence revealed that these horses were not the ancestors of modern livestock, and they represent a rather dead-end of domestication.<sup>2</sup> Further indications for the presence and nature of utilisation are sparse, ambiguous and indirect such as the anthropological analysis by Trautmann et al.,<sup>3</sup> who have recently suggested that the practice of riding began in the 3<sup>rd</sup> millennium BCE among Yamnaya culture associated societies. In the long and multi-stage process of domestication, there is clear archaeological evidence for

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<sup>1</sup>Outram et al. (2009); Outram (2023); Gaunitz et al. (2018).

<sup>2</sup>Gaunitz et al. (2018); Librado et al. (2021, 2024).

<sup>3</sup>Trautmann et al. (2023).

carriage equids from the end of the 3<sup>rd</sup> millennium BCE, whereas there is evidence for riding and milking of these horses from the first half of the 2<sup>nd</sup> millennium BCE.<sup>4</sup>

In the Carpathian Basin, and especially in Transdanubia (Western Hungary) the archaeozoological data implies that during the Copper Age (~3600–2800 BCE) in Boleráz and Baden cultures horse remains are rare, e.g. at Balatonőszöd site only ~0.6% of the recorded animal bones belonged to horses. In the following millennium the settlements of early Bronze Age Somogyvár–Vinkovci (~2600–2200 BCE), Kisapostag/Encrusted Pottery cultures (~2200–1500 BCE) also yielded similar amounts of horse remains (between 0.5 and 1.43%, up to 5% in the Middle Bronze Age), with slight increase in frequency.<sup>5</sup>

As opposed to the more scattered assemblages in other parts of Hungary, the first true evidence for horsekeeping in the region appeared on Bell Beaker culture settlements around Budapest (e.g. in Albertfalva site) towards the end of the 3<sup>rd</sup> millennium BCE.<sup>6</sup> Here the ratio of horse remains was very high (up to 60%), raising the possibility of a domestication centre, but this theory is questioned by the large number of young animals that were most likely kept for their meat.<sup>7</sup> The earliest direct evidence for horse herding through artefacts, such as antler cheekpieces, linked to riding and/or other equine utilisation practice appears in the archaeological record from the eastern part of Hungary from the 2<sup>nd</sup> millennium BCE from the settlements of the Vátya and Füzesabony cultures.<sup>8</sup> The genomic origin of these horses still remains to be unresolved, but studies, such as Librado et al.<sup>9</sup> and this one, aims to reveal the complex origin and management of these domesticated lineages.

Earlier genomic studies that relied mainly on the hypervariable region of the maternally inherited mitochondrial genomes were insufficient to reveal detailed population histories due to poor phylogeographic signals, although major trends, such as shifts in major genomic compositions were shown.<sup>10</sup> In recent years, whole genomes of ancient horses have revealed temporal and spatial distribution of dominant lineages, and the draft history of their domestication.<sup>11</sup> Accordingly, at least six major phylogenomic clusters existed in the past ~100,000 years, from which only two have remained today, the so-called DOM2, where all modern domestic breeds belong, and the descendants or close relatives of Botai/Borly horses, known today as Przewalskii,<sup>12</sup> where the Mongolian wild horses belong.

The heartland of Europe was dominated at least until the beginning of the European Bronze Age by two related and now extinct horse lineages, peaking among Iberian and Central European horses (the latter sampled from Corded Ware culture context). Other regions show a mixed populations of these, forming a natural genetic cline from Iberia to the steppes, which also creates spatial variation, e.g., those found in the Carpathian Basin belong to the HUNG group, those of the Transylvanian Basin to ENEOROM group, etc.<sup>13</sup> Horse remains with DOM2 ancestry are detectable from the Eneolithics in Yamnaya culture related archaeological context in Eastern Europe.<sup>14</sup> These steppe groups' westward expansion around ~3000 BCE and their direct transmission into the Corded Ware culture mediated a strong cultural and genetic impact on other European societies as well,<sup>15</sup> but without the introduction of DOM2 horses that happened only a thousand year later.<sup>16</sup> The replacement of the HUNG lineage in the Carpathian Basin was originally suggested by Librado et al.,<sup>17</sup> and has been recently detailed by Librado et al.<sup>18</sup> Accordingly, while the territory of today's Hungary was among the first regions where DOM2 lineages were introduced (current evidence puts this date to the 23<sup>rd</sup> century BCE), HUNG groups lasted until the end of the 21<sup>st</sup> century BCE. Based on Librado et al.,<sup>19</sup> by the end of the 19<sup>th</sup> century BCE, DOM2 lineages became ubiquitous and exclusive in the area, although the genomic makeup of the recently died out tarpan horse (~45% European, ~55% DOM2) suggests hidden survival of these lineages somewhere in the Central European regions.<sup>20</sup> In this study, we present a novel Middle Bronze Age horse genome from Vátya culture context that harbours HUNG ancestry, to diversify the picture of its replacement.

## RESULTS

The newly sequenced, ~0.9× average coverage complete horse shotgun genome (Tompal) from Tompa archaeological site from southern Hungary can be dated to 1870–1620 cal. BCE (95.4% CI, see Materials for site and radiocarbon date description). While we acknowledge and cite the results of Librado et al.,<sup>21</sup> we only co-analysed Tompal with the dataset available until the Librado et al.<sup>22</sup> for practical reasons.

<sup>4</sup>Chechushkov et al. (2018); Chechushkov et al. (2020); Wilkin et al. (2021); Bozi and Szabó (2023); Maran (2020).

<sup>5</sup>Gál (2017).

<sup>6</sup>Gál (2017).

<sup>7</sup>Dani and Kulcsár (2021).

<sup>8</sup>Bozi and Szabó (2023); Kanne (2025); Librado et al. (2021).

<sup>9</sup>Librado et al. (2021, 2024).

<sup>10</sup>Guimaraes et al. (2020)

<sup>11</sup>Librado et al. (2021, 2024); Gaunitz et al. (2018); Fages et al. (2019).

<sup>12</sup>Gaunitz et al. (2018).

<sup>13</sup>Librado et al. (2021, 2024).

<sup>14</sup>Librado et al. (2021).

<sup>15</sup>Allentoft et al. (2015); Haak et al. (2015).

<sup>16</sup>Librado et al. (2021, 2024).

<sup>17</sup>Librado et al. (2021).

<sup>18</sup>Librado et al. (2024).

<sup>19</sup>Librado et al. (2024).

<sup>20</sup>Librado et al. (2021, 2024).

<sup>21</sup>Librado et al. (2024).

<sup>22</sup>Librado et al. (2021).

## Genomic makeup of Tompa1

A set of ~1.6 million biallelic SNPs were considered for population genomic analyses, obtained from,<sup>23</sup> after applying further filters (for details, see Methods). Principal component analysis (PCA, Fig. 1a) reveals major clines among ancient and extant horses. Tompa1 clusters with the two other Bronze Age horses from Hungary, situated in an intermediate position between Neolithic and Eneolithic horses from Turkey/Romania and Czechia/Poland, reflecting the natural genomic cline of wild horses in the region.<sup>24</sup> *Struct-f<sub>4</sub>* analysis<sup>25</sup> with five components also confirms the position of Tompa1 (Fig. 1b), although it shows some similarity to Eneolithic Romanian and Turkish samples through an elevated component modelled by DOM2 horses. *f<sub>3</sub>*-analysis<sup>26</sup> shows highest similarity of Tompa1 to Bronze Age samples Duk2 and Car05 from today's Hungary (merged into one Hun\_MBA group), but *f<sub>4</sub>*-statistics<sup>27</sup> in form of *f<sub>4</sub>*(Tompa1, Hun\_MBA, DOM2, Donkey) revealed further affinity towards steppe horses. To assess, whether this extra DOM2-like component is the sign of actual mixture between local and steppe stocks or the sign of the geographic cline, we first applied *qpAdm*<sup>28</sup> analysis. Tompa1 can be modelled with *qpAdm* as two-way mixture of Hun\_MBA (c. 95–78%) and an Eastern component, providing the highest estimates for Turkey\_EBA ( $22.1 \pm 7.84\%$ ,  $P = 0.154$ ) and only  $4.78 \pm 3.06\%$ ,  $P = 0.272$  for DOM2 as fitted sources. While three-way admixture models of Hun\_MBA, Turkey\_EBA and any other steppe related population yield acceptable *P*-values, the third components are too small and standard errors are too high to consider it reliable. These results are on par with the second position of Turkey\_EBA on *f<sub>3</sub>* and previous results on Hun\_MBA,<sup>29</sup> except Tompa1 has slightly higher levels from this Anatolian-related ancestry. Considering that Tompa1 was found at the lowest latitude among Carpathian Basin horses, all these results robustly position it along a natural genetic cline between Anatolia and the Carpathian Basin.

We evaluated the origin of this component further, in order to determine whether it is part of the wild genetic structure of horses in the area, i.e. part of the NEO-ANA (Neolithic Anatolian) cline described in Librado et al.<sup>30</sup> resulted from the limited post-Last Glacial Maximum expansion of steppe horses to Europe unrelated to human activity, or whether it is the sign of minor but recent introduction of DOM2 ancestry to an already existing local livestock. In order to test this, we applied *Admixfrog*<sup>31</sup>

software to assess DOM2-like genomic chunk sizes in Tompa1 (for details, see Methods). Accordingly, Tompa1 does not show particular 'aggregation' of steppe related genomic chunks; instead, steppe related chunks are distributed evenly in small sizes roughly equally in homozygous and heterozygous form, in complete par with what one would expect from a geographic-cline induced, over longer time manifesting genetic drift (Fig. 1c), pointing to no recent introduction of DOM2 lineage into the HUNG cluster, also in line with Librado et al.<sup>32</sup>

## Population size

We performed runs of homozygosity (ROH) analysis by *ROHan*<sup>33</sup> software, to assess the general pattern of inbreeding. Unfortunately, neither Tompa1 nor the novel dataset from Librado et al.<sup>34</sup> has sufficient coverage for a proper analysis. However, Car05 and Duk2 (HUN\_MBA) do, along with a number of ancient database samples. Since the results tend to be higher ROH-skewed towards lower coverages, besides inferences on the original dataset and a set of relevant database samples (see Table 1 for samples and results), we performed this test on subsampled (down to the coverage of Duk2, ~2.7×) BAM type DNA alignment files as well, in order to see whether the general patterns across samples remain with lower coverages. Accordingly, a general pattern of increasing ROH percentages in time forward can be observed as a sign for a bottleneck that has already been shown by previous studies.<sup>35</sup> Surprisingly, Hun\_MBA and Kan22 (Turkey\_EBA) show the highest proportions for ROH segments (up to 8%), suggesting either extreme population size reduction or intensive selective breeding. While these extreme values also could be the results of lower coverages, the downsampled dataset does not show a significantly different proportion of ROH across the samples, although standard errors reach such a level that make individual evaluations ambiguous.

## DISCUSSION

According to previous studies on Late Neolithic, Copper Age and Early Bronze Age Central Europe,<sup>36</sup> the region faced extreme changes connected to human mobility<sup>37</sup> and activities connected to agricultural advancements.<sup>38</sup> Previous archaeogenomic studies and our results on Bronze Age livestock reveals diverse and colourful processes, including DOM2 introduction and local origin lineage survival in the

<sup>23</sup>Jagannathan et al. (2019).

<sup>24</sup>Librado et al. (2021, 2024).

<sup>25</sup>Librado and Orlando (2022).

<sup>26</sup>Maier et al. (2023); Patterson et al. (2012).

<sup>27</sup>Maier et al. (2023); Patterson et al. (2012).

<sup>28</sup>Haak et al. (2015); Maier et al. (2023); Petr et al. (2019).

<sup>29</sup>Librado et al. (2021).

<sup>30</sup>Librado et al. (2021, 2024).

<sup>31</sup>Peter (2020).

<sup>32</sup>Librado et al. (2024).

<sup>33</sup>Renaud et al. (2019).

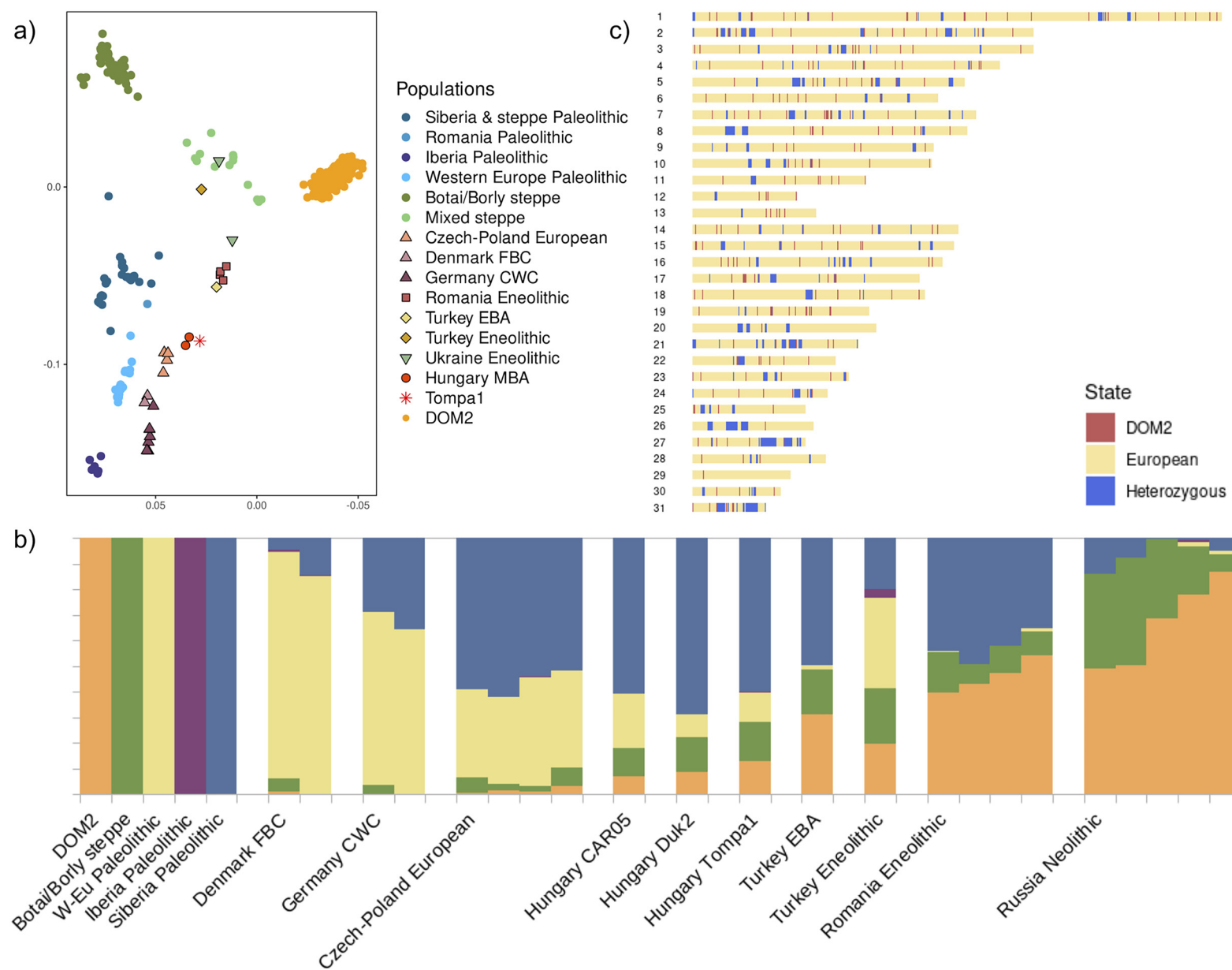
<sup>34</sup>Librado et al. (2024).

<sup>35</sup>Fages et al. (2019); Gaunitz et al. (2018); Librado et al. (2021, 2024).

<sup>36</sup>Szabó (2017).

<sup>37</sup>Allentoft et al. (2015); Haak et al. (2015).

<sup>38</sup>Gamarra et al. (2018); Gulyás and Sümegi (2011); Magyari et al. (2012); Reed (2017).



**Fig. 1.** Genomic makeup of ancient horses. a) PCA of ancient horse genotypes, prehistoric horses from Hungary have an intermediate location between Northern and Southern populations. b) Struct-f4 analysis with  $K = 5$  positions Tompa1 between prehistoric horses from Romania and Hungary. c) DOM2 genomic segment distribution on the chromosomes of Tompa1

region. Our results show a much longer survival of non-DOM2 lineage in the Carpathian Basin until the 18<sup>th</sup> century BCE, making these horses as potential candidates for tarpan horse ancestors. However, none of the tested models supported this hypothesis, revealing that pre-domestication lineages survived in at least one more territory in Europe, besides the Carpathian Basin.

A number of archaeological,<sup>39</sup> anthropological,<sup>40</sup> archaeozoological<sup>41</sup> and genetic<sup>42</sup> evidence points to at least partial domestication of non-DOM2 horses in Europe, including the studied area, but the extent and the start of this practice is highly disputable. Severe bottleneck, as indicated by ROH analysis, suggests a highly decreased population size for HUNG cluster horses in the Carpathian Basin and probably in the Balkans and Anatolia as well, at the studied period. Additionally, the fact that DOM2 and HUNG horses lived contemporaneously in the same region for at least two centuries without evidence for admixture, points to the fact that horse stocks were rigorously managed. This observation is in line with the vast difference between ROH patterns in DOM2 and HUNG horses, which also points to a severely shrinking and/or heavily managed population for the latter. While the archaeological context of Tompa1 suggests some form of horsekeeping practice for HUNG horses, the current evidence is not conclusive on this matter. Numerous scenarios can explain our data, and in our view the most likely ones are:

1. The DOM2 horses were maintained as a rigorously managed domesticated stock, whereas the wild HUNG horses persisted as scattered populations that ultimately went extinct. Additionally, some wild HUNG horses were occasionally kept alongside DOM2 individuals, but as tightly separated stocks.
2. By the studied period no truly wild stock remained, only tightly separated DOM2 and HUNG lineages, which were most likely managed in entirely different ways.

Although further scenarios are still plausible, such as DOM2 displacement of HUNG horses in the wild, but this would suggest additional, yet unknown human-influence on wild and domestic stock management, making this model less parsimonious. All the aforementioned hypotheses require further investigations, but the results of this study alone imply remarkable horse management processes in this region in the corresponding period, which opens new perspectives to archaeogenomic analyses of past horse populations.

## MATERIALS AND METHODS

### Materials and archaeological background

At Tompa archaeological site, which belongs to a settlement of the Vanya culture, a complete skull of a horse was recovered that belonged to an 8 years old mare, dated between 1870 and 1620 cal. BCE ((DeA-27707) AMS dates of  $3412 \pm 29$  BP, the  $2\sigma$  calibrated range spans 1869–1849 cal BC (4.6% probability) and 1772–1621 cal BC (90.9% probability), see Fig. 2).<sup>43</sup> The lesions observed on the incisive bone of the Tompa-1 horse clearly indicate human intervention (for details, see Bozi and Szabó).<sup>44</sup>

### Ancient DNA laboratory work

Laboratory work was performed under sterile conditions in a dedicated ancient DNA laboratory facility (Institute of Archaeogenomics, ELTE (formerly HUN-REN) Research Centre for the Humanities, Budapest, Hungary). The laboratory work was carried out while wearing protective clothing. Separate work areas were irradiated with UV-C light, surfaces were cleaned with DNA-ExitusPlus™ (AppliChem) and/or bleach. Petrous bone and tooth samples were taken from Tompa1. Sample surfaces were cleaned by sandblasting and UV-C irradiation. Bone powder was used to extract DNA from the petrous bone, and from the cementum layer of the tooth, blank controls were included at all steps. DNA extraction was performed according to Rohland et al.<sup>45</sup> on liquid-handling systems. DNA libraries were prepared using UDG-half treatment based on the 2015 protocol of Rohland et al.<sup>46</sup> with minor changes suited for

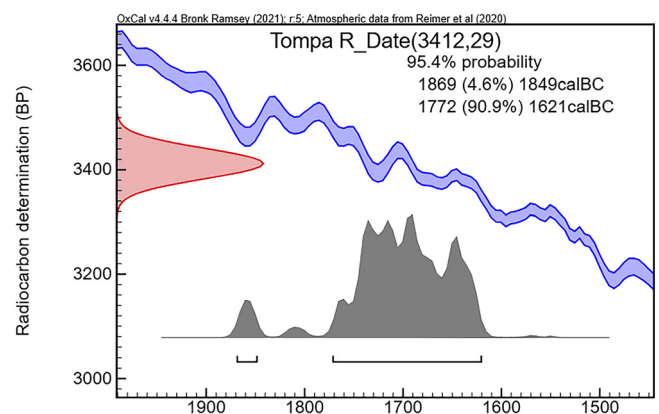


Fig. 2. Calibration curve for radiocarbon date (Reimer et al., 2020)

<sup>39</sup>Dani and Kulcsár (2021); Grigoriev (2021); Kanne (2022); Makarowicz et al. (2023); Przybyła (2020).

<sup>40</sup>Kanne (2022); Trautmann et al. (2023).

<sup>41</sup>Bökönyi (1959, 1974, 1978); Choyke and Bartosiewicz (2000, 2005); Vörös (1988); Vretemark and Sten (2005).

<sup>42</sup>Librado et al. (2021, 2024).

<sup>43</sup>Bozi and Szabó (2023), Reimer et al. (2020).

<sup>44</sup>Bozi and Szabó (2023).

<sup>45</sup>Rohland et al. (2018).

<sup>46</sup>Rohland et al. (2015).

automation on liquid-handling platforms. Unique double internal adapter combinations were used for every library. Libraries were then amplified with TwistAmp Basic (Twist DX Ltd) and purified with AMPure XP beads (Agilent). Libraries for shotgun sequencing were indexed using unique iP5 and iP7 indices.<sup>47</sup> DNA concentration of each library was measured on a Nanodrop (Thermo Scientific), fragment sizes were checked on Agilent 4200 TapeStation System (Agilent). NGS sequencing was done on an Illumina MiSeq System using the Illumina MiSeq Reagent Kit v3 (150-cycles) and on an Illumina Novaseq 6000 System (Novogene Company, China). Genomic data produced in this study was ultimately obtained from the petrous bone.

## Bioinformatic analyses

**Sequencing data processing.** Raw sequencing reads were processed through the *PAPline*<sup>48</sup> bioinformatic package with default options, where all of the sequencing libraries for a single sample were merged together. *EquCab3.0* genome assembly<sup>49</sup> was used as a reference for whole-genome analyses; mitochondrial genomes were obtained through mapping reads exclusively to the mitochondrial reference sequence from *EquCab3.0*. Species and genetic sex designation was performed using *Zonkey*.<sup>50</sup>

**Whole genome analyses.** As a background for our analyses, we downloaded all publicly available ancient horse genomes.<sup>51</sup> After producing BAMs aligned to *EquCab3.0* with *PAPline*,<sup>52</sup> we used *samtools* v1.10<sup>53</sup> to generate a pileup file. We obtained a list of variant positions available on the European Nucleotide Archive under the project name PRJEB85547.<sup>54</sup> This list contains ~23 million genomic variants of 88, mostly modern domesticated horses, from which we selected ~1.65 million representative variants by applying additional filters suitable for ancient DNA analysis. We retained only biallelic transversions of single nucleotide polymorphisms (SNPs), and we further discarded positions with a minor allele frequency (MAF) below 0.05, and positions with missing genotypes, and we set a minimum distance of 1000 bp between SNPs. Variants from the X chromosome were also excluded. We used this list of positions to generate the Eigenstrat<sup>55</sup> format pseudohaploid

genomes for population genomic analyses with *samtools* and *pileupCaller* v1.5.2.<sup>56</sup> For further necessary format conversions, we also used the *Eigensoft*<sup>57</sup> software package and *Plink1.9*.<sup>58</sup> *Smartpca* v16000<sup>59</sup> was used to perform PCA analysis, with *shrinkmode* and *lsqproject* options. The populations we used for *smartpca*: ancient DOM2, Russian Botai, Central steppe EBA, Hun\_MBA, Iberian Paleolithic, France Paleolithic, Germany Corded Ware culture context, Ural Paleolithic, Poland FBC, Russia Paleolithic (*Equus lenensis*), Romania Eneolithic, Turkey EBA, Kazakh Tersek Eneolithic, Kazakh Borly, Czech Neolithic, Russia Taymyr Paleolithic, Russia Yamnaya. We used *Struct-f4*<sup>60</sup> to infer ancestral proportions with  $K = 5$  for relevant populations, where we excluded samples with lower than  $\sim 1\times$  coverage (except Tompa1). For *f*-statistics, we used *admixture*.<sup>61</sup>

**Authors contribution:** Dániel Gerber and Anna Szécsényi-Nagy conceived and designed the experiments. Zoltán Dicső processed the sequencing data and performed the analyses. Géza Szabó and Róbert Bozi provided the Tompa1 sample and jointly evaluated the archaeological context with Gabriella Kulcsár and Viktória Kiss. Balázs Gusztáv Mende sampled the remains and Botond Heltai did the wet laboratory work. Dániel Gerber supervised the research and wrote the paper.

**Funding information:** This paper was supported by the MTA–BTK Lendület “Momentum” BASES research project (LP2023-8) hosted by the Institute of Archaeology, ELTE Research Centre for the Humanities, granted by the Hungarian Academy of Sciences.

**Data availability:** Produced sequences of the Tompa1 sample are available at the European Nucleotide Archive under project name PRJEB85547.

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<sup>51</sup>Fages et al. (2019); Gaunitz et al. (2018); Librado et al. (2021).  
<sup>52</sup>Gerber et al. (2023).  
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<sup>58</sup>Purcell et al. (2007).  
<sup>59</sup>Patterson et al. (2017).  
<sup>60</sup>Librado and Orlando (2022).  
<sup>61</sup>Maier et al. (2023); Patterson et al. (2012).

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Appendix

Table 1. ROHan results

Country/culture-period/group	Sample name	<sup>14</sup> C age (BCE)		Segments in ROH (%) + SD	Average length of ROH (Mb)	Average length of ROH + SD	Average depth of coverage	Downsampled to the coverage of Duk2 (2.72×)	
		From	To					Segments in ROH (%) + SD	Average length of ROH + SD
Russia_Scythian_IA_DOM2	Arz1x13	750	412	2.00698 (1.35371, 2.20167)	20.0	2e+06 (1.91667e+06, 2.21429e+06)	8.76	1.76367 (0, 5.64516)	1.98333e+06 (0, 3.63636e+06)
Poland_Trzciniec Culture_EBA_DOM2	PLKaz2	1,533	1,427	2.01401 (0.132159, 3.64797)	17.4	1.73913e+06 (1.48387e+06, 3e+06)	3/3	1.19628 (0, 6.45007)	1.77632e+06 (0, 2.25e+06)
Romania_Noua_culture_BA_DOM2	Gar3	1,612	1,465	1.44357 (0.568928, 2.31523)	15.8	1.57576e+06 (1.57143e+06, 2.16667e+06)	4/3	1.23675 (0, 21.288)	2.02841e+06 (0, 3.5e+06)
Moldova_BA	Molda1	2,140	1,985	2.02198 (0.184162, 9.12738)	32.9	3.28571e+06 (2.49315e+06, 4e+06)	2.86	2.02198 (0.184162, 9.12738)	3.28571e+06 (2.49315e+06, 4e+06)
Hungary_MBA	Duk2	2,140	1,977	3.31126 (0.535236, 8.10552)	21.4	2.14286e 06 (1.74227e 06, 6e 06)	2.72	3.31126 (0.535236, 8.10552)	2.14286e 06 (1.74227e 06, 6e 06)
Turkey_EBA	Kan22	2,466	2,306	8.58896 (0.747253, 12.3529)	30.6	3.0625e+06 (2.96471e+06, 5.66667e+06)	3/4	8.85853 (0, 17.9296)	2.64567e+06 (0, 3.04545e+06)
Hungary_EBA	Car05	2,571	2,344	6.33245 (0.0890076, 10.9521)	20.6	2.05556e 06 (2e 06, 2.71698e 06)	3/11	6.26655 (0, 13.6082)	1.97015e 06 (0, 2.67925e 06)
Russia_Yamnaya_BA	RN58	2,879	2,636	0.174978 (0, 1.72884)	13.3	1.33333e+06 (0, 2.71429e+06)	2/9	0.174978 (0, 1.72884)	1.33333e+06 (0, 2.71429e+06)
Russia_Repin_Eneo-BA	LOR18x09	3,265	2,913	0.43573 (0.13089, 0.790514)	13.8	1.38462e+06 (1.25e+06, 3e+06)	4/26	0.21796 (0, 7.44841)	2.34921e+06 (0, 2.5e+06)
Kazakh_Tersek_Eneo	Besta7	3,328	2,936	0.392157 (0.218055, 0.524934)	18.0	1.8e+06 (1.66667e+06, 2e+06)	10.56	0.655594 (0.13363, 1.71946)	2.53333e+06 (2.5e+06, 3e+06)

(continued)

Table 1. Continued

Country/culture-period/group	Sample name	<sup>14</sup> C age (BCE)		Segments in ROH (%) + SD	Average length of ROH (Mb)	Average length of ROH + SD	Average depth of coverage	Downsampled to the coverage of Duk2 (2.72×)	
		From	To					Segments in ROH (%) + SD	Average length of ROH + SD
Kazakh_Botai_Eneo	Botai4	3,334	3,030	0.523332 (0, 0.970874)	14.7	1.46667e+06 (0, 1.71429e+06)	3/5	0.436872 (0, 1.90996)	2.5e+06 (0, 2.8e+06)
Czech_Eneo	PRA18	3,350	3,102	2.66785 (0, 20.9329)	21.4	2.13953e+06 (0, 3.15789e+06)	2.75	2.66785 (0, 20.9329)	2.13953e+06 (0, 3.15789e+06)
Czech_FunnelBeaker_Eneo	PRA84	3,364	3,108	2.2261 (0.91663, 2.6643)	17.6	1.76471e+06 (1.7e+06, 2.1e+06)	6.95	2.48691 (0.875657, 2.94906)	1.83333e+06 (1.72727e+06, 2.85714e+06)
Kazakh_Tersek_Eneo	UR17x80	3,364	3,105	0.742034 (0, 2.92867)	28.2	2.81818e+06 (0, 4.25e+06)	2.87	0.742034 (0, 2.92867)	2.81818e+06 (0, 4.25e+06)
Kazakh_Borly_Eneo	Borly1	4,533	4,364	1.75208 (0.135808, 4.38886)	30.0	3e+06 (2.65714e+06, 4.44444e+06)	3	1.9685 (0, 13.1148)	2.06897e+06 (0, 4.09091e+06)
Russia_Orlovka_Eneo	Var3	5,616	5,482	2.74629 (1.35727, 3.44057)	21.7	2.17241e+06 (2.08108e+06, 3.44444e+06)	3.91	2.29277 (0.406688, 7.44681)	3.46667e+06 (2.23188e+06, 9e+06)
Turkey_Eneo	KSK16232	6,396	6,241	4.27313 (0, 6.71046)	17.6	1.70238e+06 (0, 1.76364e+06)	6/8	7.84672 (0, 100)	1.89011e+06 (0, 3.25301e+06)
France_Paleo	Gral7	19,941	19,398	1.0898 (0.218627, 1.9573)	19.2	1.92308e+06 (1.91304e+06, 2.5e+06)	3/5	1.13686 (0, 2.28206)	2.16667e+06 (0, 2.77778e+06)
Russia_Paleo	RN130	21,301	20,988	0.610022 (0.262123, 1.23511)	28.0	2.8e+06 (2e+06, 3e+06)	3/2	0.784998 (0, 1.1654)	2.88889e+06 (0, 3e+06)
Belgium_Goyet_Paleo	Vert311	35,104	33,524	0.305144 (0.131291, 0.483092)	26.0	1.83333e+06 (1.75e+06, 3e+06)	3/4	0.174444 (0.0886525, 0.9839)	3.66667e+06 (2e+06, 4e+06)

Samples in bold are the regionally and chronologically most relevant samples to Tompa1.