Ancient equine genomes reveal dawn of horse domestication

An analysis of ancient genomes reveals an explosive geographical and demographic spread of modern domestic horses about 4,200 years ago. The findings counter the idea that horses accompanied and mobilized the mass migration of humans from the Eurasian steppes about 5,000 years ago.

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The problem

Modern domestic horses originated in the western Russian steppes[1]. However, the timeline of domestication remains debated, because the earliest archaeological evidence for the corralling, harnessing and milking of horses has been found outside that region, in Central Asia[2]. The exact chronology for the widespread use of horses for transport is also contentious[3]. Paramount to this controversy is whether horseback riding developed in Yamnaya societies, thereby supporting the mass migration of this population from the steppes about 5,000 years ago[4]. Yamnaya people are thought to have spoken an ancestral Indo-European language rich in horse-related terminology, suggesting that they had established horse domestication. Rare skeletal alterations that develop in lifelong horseback riders have been found in Yamnaya[5], and even earlier, contexts. However, evidence suggests that the movement of horses was limited during the mass migration of the Yamnaya, which hardly aligns with the idea of people on horseback[1,3].

The solution

We performed radiocarbon dating and next-generation genome sequencing on equine remains from 230 Eurasian archaeological sites, to generate a detailed overview of the genetic make-up of horses in the regions and during the periods at the heart of these controversies. The regions include the Botai settlement in Central Asia, which hosts the earliest potential evidence of horse domestication, and parts of Europe into which Yamnaya people and their descendants moved.

We searched our extensive genome time series for the earliest genetic signatures of husbandry to clarify the timeline of horse migration and the emergence of breeding practices and large-scale stock production. Migration and demographic expansion were inferred using state-of-the-art methodology. An innovative method was devised to identify when younger animals suddenly started to be used for breeding — an indicator of the need to accelerate production and meet demand — thereby reducing the interval between successive horse generations.

All our lines of evidence were remarkably aligned, indicating that horses underwent an explosive demographic and geographical expansion across Europe about 4,200 years ago. Earlier human migrations from the steppes were not followed by those of horses, and preceded the emergence of modern domestic horses (Fig. 1a). Intervals between generations also became considerably shorter about 4,200 years ago, leading to an exponential increase in horse production (Fig. 1b). The only evidence for an earlier, sudden change in generation times was found in Botai, reinforcing the idea that another horse bloodline was domesticated about 5,500 years ago.

The implications

The extraordinary success of a single bloodline about 4,200 years ago has no equivalent in earlier time periods. It points to the emergence of an era in human history in which horses considerably accelerated mobility and connectivity. Our work also implies that it took about 500 years to breed this new type of horse from a limited foundational stock of a few hundred animals. Nevertheless, archaeological and genomic evidence at Botai strongly suggests that another group of people had previously engaged with horses. Given that the Botai horses remained in Central Asia, their domestication was probably for food, rather than mobility.

Importantly, our data do not provide sufficient resolution to ensure that local shifts in horse migration can always be detected — any development of domestication before about 4,200 years ago might not have left genomic signatures if it did not involve substantial numbers of horses or breeding techniques that accelerated generation times and increased productivity. Changes in the nature of human–horse relationships, such as the attribution of spiritual power or symbolic status to horses, would also remain undetected in horse genomes, even though such relationships are integral elements of many past societies and cultures.

Future work will fill the remaining knowledge gaps in the past and present genetic diversity of horses. Analyses of other proxies for the origins, management and movements of horses — such as analyses of isotopes in equine remains that indicate diet and mobility, and the metal composition of equipment buried with horses — will shed further light on the complex historical development of horse handling.

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EXPERT OPINION

"Librado and colleagues' work presents another important chapter in the history of horse domestication. The large international team presents new genome data from 124 ancient horses and 140 new radiocarbon dates. On integration with published genome data from ancient horses and modern-day domestic breeds, these new data account for a very powerful time series that informs directly on many critical aspects of horse domestication." (CC BY 4.0)

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FIGURE

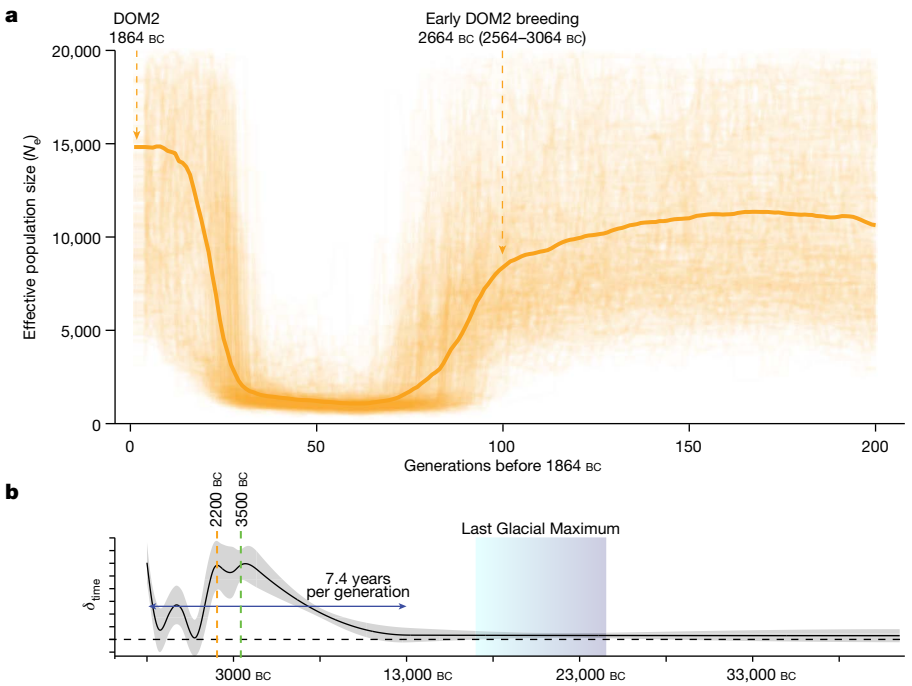


Figure 1 | Genetic evidence of early horse breeding. a, An analysis of ancient horse genomes was used to estimate the effective population size (N_e; the number of individuals that effectively participated in producing the next generation) of the lineage that led to modern domestic horses (DOM2). The earliest DOM2 horses identified in the genomic data set were from around 1864 BC. The thick line is the average of replicates (thin lines) of the statistical analysis, which was done using minor variations in data sampling. **b**, δ_{time} is a measure of the estimated time between generations of horses. The double-headed arrow indicates the average generation time during the past 15,000 years. Peaks mark the introduction of breeding practices that expedited horse production. The shaded band represents the 95% confidence interval for the regression analysis performed. Last Glacial Maximum, 17,000–24,000 BC. Librado, P. *et al.*/*Nature* (CC BY 4.0).

BEHIND THE PAPER

This work started after we noticed that some ancient horse genomes carry more mutations than would be expected if the rate of evolution had been constant. This might have reflected an acceleration in the yearly mutation rate during domestication, for instance. Proving this theory was challenging and, at times, we despaired because our methodology estimated unrealistic generation intervals until it was fully developed. It took hard work to build this line of evidence and to validate our conclusions through computer simulations. Generating the necessary data was also time-consuming. Moreover, as we were doing our research, the idea that Yamnaya migrations were linked to horse riding was revived. This project has truly been an emotional roller coaster, which made it extremely satisfying when all the evidence finally aligned.

P.L. and **L.O.**

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FROM THE EDITOR

By timing the domestication of the modern horse bloodline, this study makes an important contribution to the literature on human history. The authors have assembled a valuable data set and provide innovative tools for the inference of breeding practices that will be useful for follow-up studies.

Michelle Trenkmann, Senior Editor, *Nature*