The genomic origins of the modern domestic horse

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The horse (Equus caballus) is one of the last large herbivores to have been domesticated. It, however, perhaps represents the animal species that most impacted human history. It provided humans with the capacity to travel faster than they could on their own legs and to truly globalize the exchange of genes, cultures, and diseases for the first time until the recent mechanization of the world during the 20th century. The horse also revolutionized warfare with the development of chariotry in the early Bronze Age and the rise of mounted cavalry in the early Iron Age while it provided vital support for farmers from the Middle Ages onwards. The breadth and number of services that were provided by horses are in striking contrast with our limited understanding of their origins as the archaeological evidence for their exact domestication timing and homeland have remained contentious. To clarify the evolutionary origins of the domestic horse, we have leveraged methods at the forefront of ancient genomics to characterize the population structure of wild horses prior to, during, and after domestication. The 264 ancient horse genomes sequenced represent the largest collection of genomes for a non-human organism. They revealed a Eurasian continent playing host to multiple divergent genetic lineages, isolated by distance and by major geographic barriers and ecozones until 4,200 years ago, a time when one single genetic lineage became suddenly widespread. This genetic lineage was originally confined to the lower Don-Volga region but gave rise to the more than 600 domestic breeds now living around the world. This unveils the western Russian steppes as the genetic homeland of the modern domestic horse. A genomic scan for signatures of positive selection identified two genetic changes at the ZPMF1 and GSDMC loci that were instrumental to the success of early domestic bloodlines. The associated biological functions suggest behavioral changes facilitating taming and social interactions, and a stronger lumbar anatomy, potentially alleviating the pain resulting from horseback riding and chariot drawing. Interestingly, the genetic expansion of the new domestic bloodline could be mapped with the spread of spoke-wheeled chariots and the massive migration associated with the Sintashta material culture, and the expansion of Indo-Iranian languages in Asia. In Europe, however, the spread of the domestic horse occurred more than 500 years after the migration of steppe herders associated with the Yamnaya material culture. These people are generally considered the speakers of the proto-Indo-European language. Therefore, our data reject the commonly-held narrative associating horseback riding and the first expansion of Proto-Indo-European speakers outside their steppe homeland, which ultimately gave rise to the largest language family spoken on the planet.
The present work demonstrates the power of ancient genomics for reconstructing the complex processes accompanying the early stages of animal domestication and the further expansion of past civilizations. Such processes can no longer be deciphered from the genetic variation. present in living animals due to the extensive selection, admixture and animal translocations that followed the emergence of modern breeds during the last two centuries.