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Horse origins turned upside-down

Only a limited number of key transformative changes have truly revolutionized human history. The domestication of the horse is one of them. Horseback riding allowed us to travel well above our own speed, spreading our genes, diseases and culture over vast geographical regions. The development of cavalry has also been paramount to the battlefield until the mechanization of weaponry and many conquerors are remembered as exceptional horse masters. Alexander the Great and Genghis Khan are perhaps the most famous. Some of their horses, such as Bucephalus, are no less legendary. The earliest archaeological evidence for horse domestication is found some ~5,500 years ago in the steppes of Central Asia, where people associated with the Botai culture engaged with the horse like no one before. Current models predict that all modern domestic horses living today descend from the horses that were first domesticated at Botai and that only one population of wild horses survived until now: the so-called Przewalski's horse, native to the Mongolian steppes. A new international study published today in the scientific journal *Science*, and led by Professor Ludovic Orlando, shows that it is unlikely to be the case and changes our view on the origins of modern horses.

Early horse domestication



Copyright: Alan Outram. Excavation at the Botai site, Northern Kazakhstan, 2017



Copyright: Alan Outram. Modern domestic horse herd in northern Kazakhstan, 2016

“There is a lot of evidence in the archaeological record demonstrating that Botai horses were husbanded”, says Alan Outram, Professor of Archaeological Science at the University of Exeter. Professor Outram and Professor Victor Zaibert have carried out archaeological excavations at Botai for over two decades and have discovered unambiguous signs of domestication. Some of the horse teeth excavated show traces of bit wear, suggesting that at least some of the horses were harnessed. Isotopic analysis of the fat residues in pottery shows evidence of horse milking. “It is not just horse meat that Botai people consumed, but also mare’s milk”, adds Professor Outram. Additional excavation work carried out as part of the new study now reveals that Botai people built corrals to keep horses in numbers, close to their habitations. “It was essential to Botai people to manage the horse resource as it provided the basis of their subsistence strategy. Probably horses were even first domesticated at Botai because horse riding somehow facilitated horse hunting.”, concludes Professor Outram.

Transforming wild animals into domesticates

With compelling evidence supporting domestication, and a geographic location within the steppes of Central Asia – a natural environment for the animal, Botai horses were often assumed to be the source of all domestic horses. Therefore, when Orlando’s research team embarked on sequencing the genomes of Botai horses, they aimed at characterizing the genome sequence of the ancestors to all modern domesticates. “Horse breeders have considerably transformed the horse during history, especially during the last few centuries with the development of intensive selective breeding. It is thus almost impossible to reconstruct early stages of horse domestication by looking at the genome of modern horses.” says Ludovic Orlando, Professor of Molecular Archaeology at the University of Copenhagen, Denmark and Research Director at the CNRS, University of Toulouse, France.



Copyright: Daron Donahue & Niobe Thompson. Clearwater documentary. Ludovic Orlando sampling the remains of Botai horses, Kazakhstan, August 2016.

In a recent work (see <http://science.sciencemag.org/content/356/6336/442>), his team reconstructed the genomes of Scythian horses and clearly established that the genome of the animal has been dramatically modified during the last 2,000 years. This time, by targeting the Botai horses, the team aimed for a deeper time travel, some 5,500 years ago. “Sequencing the genomes of the earliest domestic horses would catch evolution red-handed at the time we first tamed wild horses. It would thus reveal the biological changes underlying the process of animal domestication as it started.”, he adds.

A feral horse, after all

The analysis of the genome data, however, revealed an extraordinary finding. Rather than being the source of modern domesticates, the Botai horses appeared to be the direct ancestors of another group of horses that lived in Kazakhstan some ~5,000 years ago and of... Przewalski’s horses! It looks like the latter, which were taken to be the last wild horses in the planet since their first discovery in the 19th century, actually represent the feral descendants of the first horses ever domesticated. “Our findings literally turn current population models of horse origins upside-down: what we used to understand as the last wild horse on earth is in fact the descendant of the earliest domestic horses, which simply escaped human pressure and became feral during the last few millennia.”, adds Prof Orlando.



Copyright: Ludovic Orlando. A Przewalski’s horse at the Khomyn Tal reintroduction reserve, Mongolia, May 2014. The Khomyn Tal reintroduction reserve is managed by the TAKH Association pour le cheval de Przewalski (<http://www.takh.org/en/>).



Copyright: Ludovic Orlando. A Przewalski’s horse at the Khomyn Tal reintroduction reserve, Mongolia, May 2014. The Khomyn Tal reintroduction reserve is managed by the TAKH Association pour le cheval de Przewalski (<http://www.takh.org/en/>).



Copyright: Bazartseren Boldgiv. Przewalski’s horses at the Hustai National Park, Mongolia, January 2014.

The study takes advantage of the extensive genome dataset produced to identify the genomic changes underlying this feralization process. One such change affects a variant of the TRPM1 gene involved in leopard spotting, which used to be present amongst Botai horses but was eliminated from the Przewalski's horse gene pool. As such a variant is also associated with color night blindness, it is likely that it could only be artificially maintained by human herders but was rapidly lost by natural selection after the horse turned feral.



Photograph by Ludovic Orlando, reworked by Sean Goddard and Alan Outram. Artistic reconstruction of Botai horses based on genetic evidence. Some of the Botai horses were found to carry genetic variants causing white and leopard coat spotting patterns

“Ironically, we used to think that the endangered population of Przewalski's horses should be preserved as the last wild horses in the planet. We now find that they must be preserved as the closest descent of the earliest domestic horses”, says Charleen Gaunitz, one of the two PhD students in the Orlando team, who carried out the experimental work for the study.

The origins of modern domesticates

In addition to revisiting the evolutionary origins of Przewalski's horses, the study also reveals that Botai horses are not the ancestors of modern domesticates. Instead, their origin must be sought in other ancient populations. “With the genome data that we currently have, it is impossible to locate the source that gave rise to the modern horse”, says Orlando. What is clear though, is that none of the ancient Eurasian horses that the team has analyzed so far within the last ~4,100 years relates to Botai. Patterns of mitochondrial DNA variation also indicate that the horse population expanded drastically between ~4,100 and ~5,000 years ago. It thus looks like humans somehow encountered and developed a new type of horses at that time, and that this horse became extremely popular and perhaps even facilitated the expansion of human populations.



Copyright: Ludovic Orlando. Horse herder in the Khomiin Tal region, Mongolia, May 2014.

“We are looking at a series of candidate places that are known sources of major human expansions in the third millennium BCE”, says Orlando. Interestingly, the earliest fossils presently sequenced of this new horse type come from Hungary, Romania and the Pontic Caspian steppe. The team now thus does not dismiss a possible origin outside Central Asia. “This work clearly illustrates the power of harnessing ancient genome sequencing. It really allows us to discover a series of key evolutionary processes that have left little signature in the genomes of living populations.”, says Antoine Fages, the second PhD student in the Orlando team, who carried out the experimental work for the study. “Ancient genomics just rejected Botai as the ancestors of modern domesticates. We are confident that ancient genomics will soon help identify the tempo and locus of horse domestication.”, concludes Professor Orlando.

The article “Ancient genomes revisit the ancestry of domestic and Przewalski's horses” by Gaunitz and colleagues is published in Science 22nd February 2018 (<http://science.sciencemag.org/cgi/doi/10.1126/science.aao3297>). This work was supported by the European Research Council (PEGASUS #681605, <http://orlandoludovic.wixsite.com/pegasus-erc>), the Villum Fonden miGENEPI, the Danish Council for Independent Research, Natural Sciences (4002-00152B), and the Initiatives d'Excellence Chaires d'attractivité, Université de Toulouse (OURASI). It involved the contributions from an international team of 47 researchers across 28 institutions.

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