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Almost All Modern Horses Descended From A Few Oriental Stallions



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Thanks to horse breeding practices, nearly all modern horses, whether they are champion racehorses or ordinary plowhorses, trace their lineage back to the same male ancestor



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Garant 20, a purebred black Akhal-teke stallion.

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Nearly all modern domestic horses, from 2014 Triple Crown champion, American Pharoah, and ghostly Lipizzaner stallions performing horse ballet in front of spellbound crowds, to carriage horses pounding the pavement in New York City, descended from only a few “Oriental” stallions brought to Europe roughly 700 years ago. This is according to an international team of scientists who analyzed the Y chromosomes of more than 50 horses representing 21 breeds.

This study reveals how choices made long ago by horse breeders who lived during the birth of the Ottoman Empire and during Europe's Medieval period had an outsized influence on most horse breeds found throughout the world today.

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“Our data therefore illuminate the enormous impact modern horse breeding strategies -- characterized by strong selection of males and the import of Oriental stallions -- during the past few hundred years had on Y chromosome diversity,” said molecular biologist and lead author of the study, Barbara Wallner, of the [University of Veterinary Medicine](#) in Vienna.





La Mirage, a purebred gray Arabian stallion.

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Strong sex-biased selection severely limited Y chromosome lineages

More than any other domestic animal, horses are remarkable because hidden in their DNA are two dramatically different family histories -- histories based on sex.

Mitochondrial DNA (mtDNA) tells the story of the female line, whereas the Y chromosome contains the history of the male line. In domestic horses, the female lineage captures a lot of genetic diversity -- a lot of stories. This contrasts starkly with the male-specific region of the Y chromosome (MSY), which, in the case of domestic horses, has extremely low diversity ([ref](#)).

The MSY carries only a few essential genes that influence male development. The MSY is passed from fathers to sons to grandsons and thus, tracing its lineage of inheritance provides a clear path for male genealogy.

But this extremely low MSY diversity has made it nearly impossible to distinguish between individuals and lineages, and this has thwarted previous attempts to reconstruct the genetic history of stallions.

But Dr. Wallner and her team circumvented this problem by using deep, next-generation sequencing, a methodology that relies on a high number of replicate "reads" of each region within a given sequence, thereby increasing the accuracy of the sequences. This technique allowed Dr. Wallner's team to identify even the tiniest changes in a gene's sequence.

No biological process is perfect, so small mistakes can be made in a genetic sequence when it is copied. These copying errors, or mutations, in MSY genes

are rare, but once they occur, they are inherited. They are known as “polymorphic markers” because research scientists can use them to identify specific individuals and their progeny.

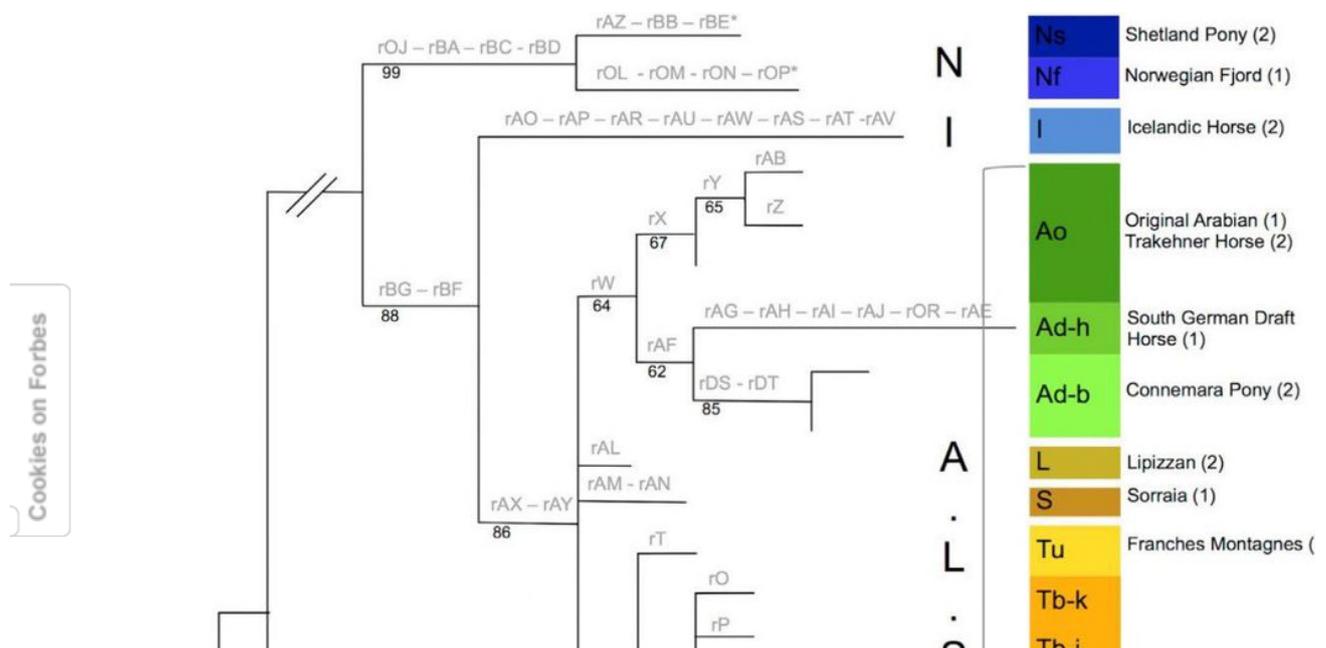
“Since random mutations accumulate over time, males who originate from a common patrilineal ancestor will share a particular collection of Y chromosome mutations,” Dr. Wallner explained in a press release.

Dr. Wallner's team used these “polymorphic markers” to identify specific haplogroups. A haplogroup is a collection of genes, such as those located on the MSY, that are inherited from only one parent.

Polymorphic DNA markers made it possible to identify individual stallion lineages

To do this research, Dr. Wallner and her team sequenced the MSY from 52 individual horses representing 21 breeds and used these polymorphic markers to track stallion geneologies. The study horses included Thoroughbreds, Arabians, Quarter horses, Lipizzaners, Norwegian fjord horses, Icelandic horses, and Trakehners along with a number of other so-called warmblooded horse breeds.

Dr. Wallner and her team used MSY sequences from all these animals to construct a family tree for the MSY gene region (Figure 2):



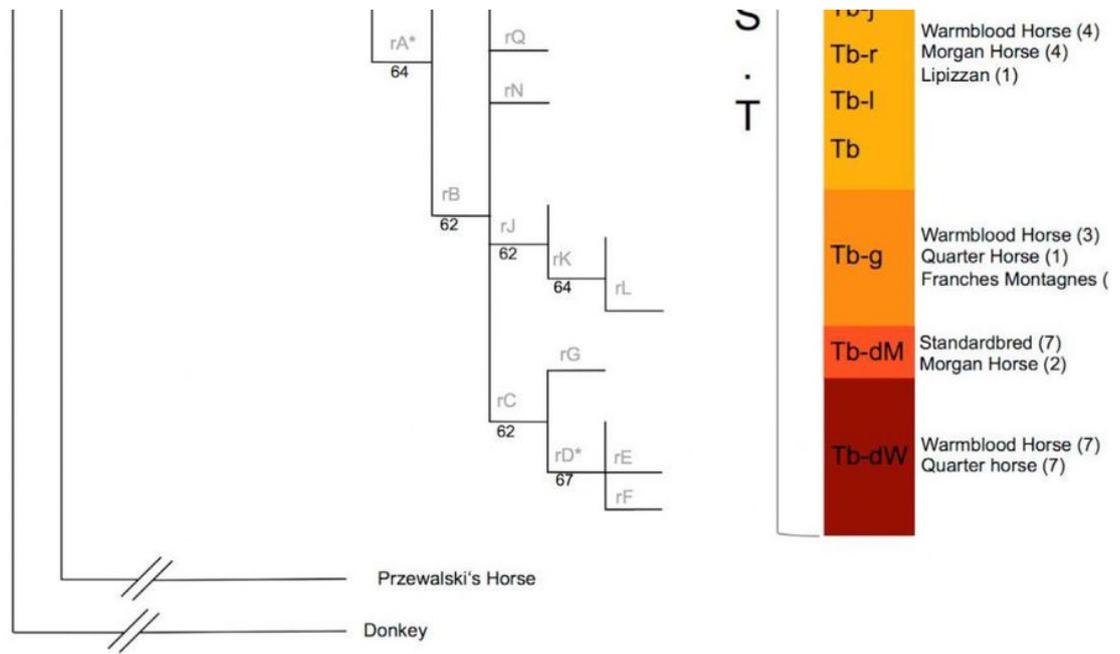


Figure 2. Maximum-Parsimony Tree of the Horse MSY from 52 Individuals

HT-defining mutations are indicated on branches, and the four mutations already described are marked with an asterisk. Bootstrap confidence values (500 replicates) are given on branches, and haplogroups are distinguished by colors. Source breeds are listed for each haplogroup, with number of samples per breed in parentheses. (doi10.1016/j.cub.2017.05.086) DOI: 10.1016/J.CUB.2017.05.086

As you can see, this gene tree captures two deep splits in MSY ancestry between northern European horses (N; Shetland ponies, dark blue; and Norwegian fjord horses, medium blue; Figure 2) and their closest relative included the study group, the Icelandic horse (I; light blue; Figure 2).

The MSY genealogy for the remaining group is so entangled that it is not possible to decipher when the four main branches (A, L, S, and T) popped up. This multi-branched group, which included 37 of the 52 samples, may not be resolvable because all but one of the breeds that it represents have an English Thoroughbred stallion somewhere in their male lineages.

Almost all modern horse breeds clustered into one 700 year old haplogroup

Using calculations based upon an estimated slow, medium or fast genetic mutation rate per generation, Dr. Wallner and her team concluded that the modern horse MSY arose from a single founder stallion that lived after horses had been domesticated.

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Combining their MSY data with written records, the researchers concluded that, except for a few Northern European haplotypes, all modern horse breeds included in their study clustered into one 700 year-old haplogroup. This haplogroup includes two major lineages: one that originated from the Arabian lineage from the Arabian Peninsula and the other from the Turkoman horse lineage from the steppes of Central Asia (Figure 4):

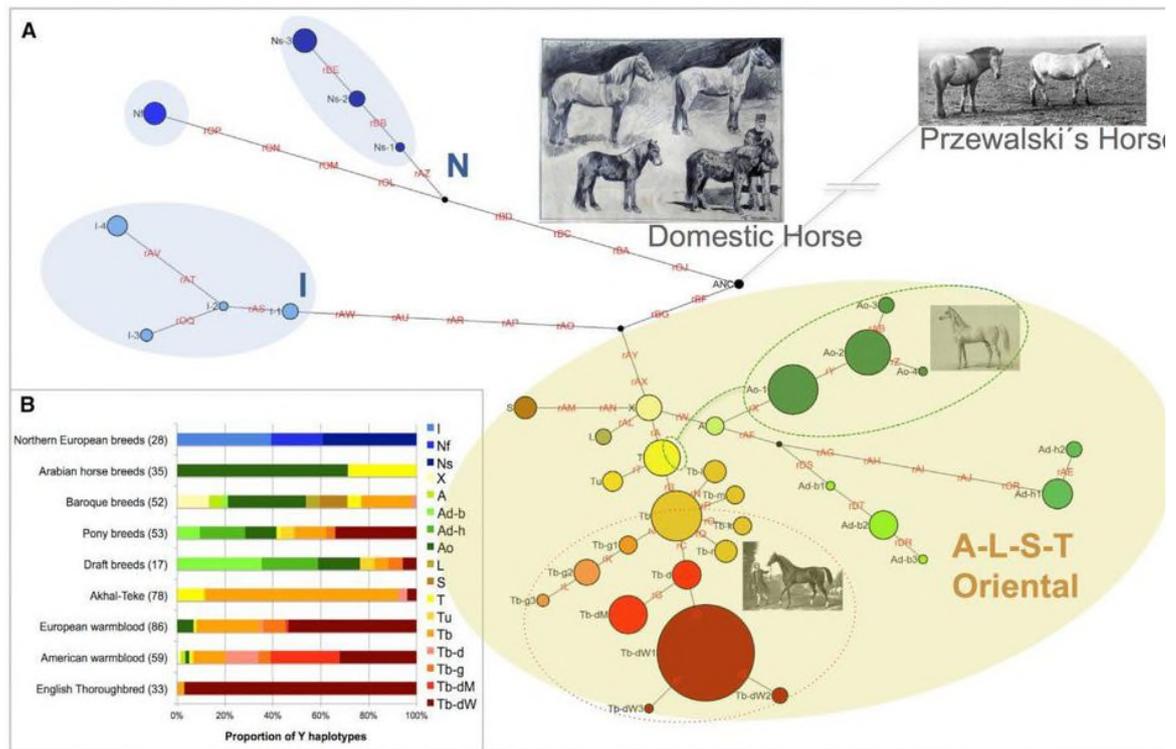


Figure 4. MSY HTs Detected in 363 Purebred Horses of 57 Breeds

(A) Median-joining network. The size of each circle reflects the sample size of each HT. Haplogroups with confirmed Original Arabian ancestry are indicated by a dotted green line, and those with English Thoroughbred ancestry are indicated in red. Mutations are given on the branches. (Images: Przewalski Horse, domestic horse, and Bairactar: Archiv Otto Antonius, Tiergarten Schönbrunn; Darley Arabian by John Wotton, Wikimedia Commons.)

(B) Relative frequency of MSY HTs in different breeds and groups of breeds. The number of samples for each group of breeds is given in parentheses.

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“Apart from stallion lines in Northern European breeds, all stallion lines detected in other modern breeds derive from more recently introduced Oriental ancestors,” Dr. Wallner said.

Inbreeding and linebreeding practices became increasingly popular seven hundred years ago when medieval horse breeders bred their local mares to a very few imported stallions ([read more](#)).

“Of particular importance was the trend to import stallions from foreign studs to improve local herds,” the authors write.

Breeders imported these stallions because they were beautiful, and because horse breeders wanted to produce a new generation of horses that were faster, stronger and lighter.

“In central Europe, this practice started in the 16th century with the popularity of Spanish and Neapolitan stallions,” write the authors. “Until the end of the 18th century, the Central European horse population was shaped by the introduction of ‘Oriental stallions’.”

This practice is similar to what we see in cats and dogs ([read more](#)). Like horses, just a few key lineages are at the root of most breeding efforts. But unlike horses, cats and dogs bred with local native species, and that gave rise to the variety of breeds seen today.

English Thoroughbred founder stallions can be traced back to a Turkoman stallion

In their quest to breed ever faster and more athletic racehorses, these imported Turkoman stallions were bred to local mares, who were already respectably fast ([read more](#)). After this infusion of “Oriental blood”, the English Thoroughbred studbook was closed in 1793 so horses with outside bloodlines -- even the offspring of “Oriental” stallions -- could not be registered.

Combining their newly obtained genetic data with pedigrees recorded by studbooks, Dr. Wallner and her team could reconstruct the paternal line of the three founders of English Thoroughbreds; the Darley Arabian (1700), the Byerley Turk (1680), and the Godolphin Arabian (1724). Their samples included 110 descendants of the Darley Arabian, 22 of the Byerley Turk, and seven of the Godolphin Arabian.

They found only one MSY lineage. This, they named the ‘Eclipse variant’ because it traces back to the English Thoroughbred stallion, named Eclipse.

This widely distributed lineage reflects the historic influence of this Thoroughbred line in horse breeding: almost all English Thoroughbreds and nearly half of all modern sport horse breeds carry the Eclipse variant.



2014 Triple Crown winner, American Pharoah, is a descendant of Eclipse. American Pharoah and jockey Victor Espinoza win the 2014 Belmont Stakes to become only the 12th Triple Crown winner in history -- and the first since Affirmed won in 1978. (Credit: Mike Lizzi / CC BY-SA 2.0) MIKE LIZZI VIA A CREATIVE COMMONS LICENSE

The research team ultimately traced the founding stallions of English Thoroughbreds back to Turkoman horses, a breed that now is extinct.

“Arabian, Turkoman, Spanish and Northern European founders can be clearly distinguished,” Dr. Wallner said.

They found that the haplogroup marker, Tb, is not present in Arabian, Spanish or Barb horses, but it was present in 81% of the 78 male Akhal-Teke included in their study (Figure 4B).

Some experts think the Akhal-Teke is a variant of the Turkoman horse -- and it's certainly easy to see the resemblance between the Akhal-Teke and the Thoroughbred -- the long legs and back, the steeply sloping shoulders, and the slender, athletic build.

“The purest descendant of the Turkoman horse today is the Akhal-Teke,” Dr Wallner agreed.



Free jumping a purebred Akhal-Teke stallion, Dirkhan.

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It's also interesting to note that the Tb haplogroup and its sub-branches was found in breeds with no documented English Thoroughbred influence, such as the Hucul and Lipizzaner stallion lines. Thus, Dr. Wallner and her team concluded that Tb appeared long before these modern horse breeds, and thus, it is probably of Turkoman origin although it was later spread widely by English Thoroughbred stallions.

Stallions experienced the most intense selection of any domestic animal

This study documents the severe selection process that early horse breeders used to improve their herds by showing how few stallion lineages actually survived. This contrasts with findings from prehistoric horse remains, which

indicate they had much more Y chromosome diversity than do modern horses ([read more](#); [ref](#)).

Further, these MSY findings contrast sharply with mitochondrial DNA, which is passed unchanged from females to their offspring. Mitochondrial DNA is especially diverse in horses, indicating modern horses had many female ancestors.

Now that Dr. Wallner and her team have developed this MSY gene tree for horses, and combined their data with pedigree information to trace the genealogy of Thoroughbred stallions, what do they plan to do with it?

“Our results pave the way for a fine-scaled genetic characterization of stallion lines, which should become routine in the near future,” Dr. Wallner said.

As Dr. Wallner demonstrated, polymorphic MSY markers can be used to trace the history and precise relationships of any stallion in detail back to their founders. Even mustangs, those iconic free-roaming horses of the American West that originated from Spanish horses, probably descended from one of these “Oriental” lineages.

“The Y chromosome data clearly show the influence of stallions from the Middle East to European and American breeds and the Y chromosomal network will serve as a useful backbone in further classification of stallion lines in various breeds,” Dr. Wallner said.

The research team is now creating a global Y chromosome “network” that will also incorporate data from rural horses that, they believe, may lack recent influences from Oriental stallions. Once these MSY genealogies are added to the network, it will be possible to identify the origin of founder stallions and to resolve their influence on the global horse population.

Dr. Wallner and her team are also collecting DNA from ancient horses to see if their Y chromosomes may provide insight into when and where wild horses were first domesticated, and to understand the domestication process from the male perspective.

Source:

Barbara Wallner, Nicola Palmieri, Claus Vogl, Doris Rigler, Elif Bozlak, Thomas Druml, Vidhya Jagannathan, Tosso Leeb, Ruedi Fries, Jens Tetens, Georg Thaller, Julia Metzger, Ottmar Distl, Gabriella Lindgren, Carl-Johan Rubin, Leif Andersson, Robert Schaefer, Molly McCue, Markus Neuditschko, Stefan Rieder, Christian Schlötterer, and Gottfried Brem (2017). **Y**

Chromosome Uncovers the Recent Oriental Origin of Modern Stallions, *Current Biology*, published online on 29 June 2017 ahead of print | doi:[10.1016/j.cub.2017.05.086](https://doi.org/10.1016/j.cub.2017.05.086)

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