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Derleme

Domestication and Origins of the Modern Horse Breeds

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Abstract

In this review, the effects of domestication on horses and various studies on the genetic origin of present domestic horse breed were compiled. Human-animal relations started to have a certain system with domestication and gradually evolved into present animal husbandry. Various changes in various species with domestication have also enabled the development of current modern animal husbandry and modern animal breeding science. There are many debates about both the domestication and origin of horses, which have had a special area among animals since the day they were domesticated. Thanks to the new technologies being used in many scientific fields such as archeology, paleontology, zoology and veterinary medicine and the advancing genetics, a long way has been achieved about the origin of the horse species and its domestication process. New information has been obtained about the origins of the horse domestication process, which is thought to have started in Central Asia about six thousand years ago, and the origins of today's domestic horse breeds. In recent studies, the domestication regions and genetic origins of horses have been reshaped, and the filial structure of horse species has changed.

Evciltme ve Günümüz Evcil Atlarının Genetik Kökeni

Özet

Bu çalışmada evciltmenin atlar üzerine olan etkileri ile günümüz evcil at türünün genetik kökenine dair yapılan çeşitli çalışmalar derlenmiştir. İnsan hayvan ilişkileri, evcilleştirme ile belirli bir sisteme sahip olmaya başlamış ve giderek günümüz hayvan yetiştiriciliğine evrilmiştir. Evcilleştirme ile birlikte çeşitli türlerde meydana gelen çeşitli değişimler günümüz modern hayvancılığının ve modern hayvan yetiştirme biliminin gelişmesini de sağlamıştır. Çiftlik hayvanları içerisinde evciltildiği günden beri özel bir alana sahip olan atların gerek evciltilmesi gerekse kökeni hakkında pek çok tartışma yürütülmektedir. Arkeoloji, paleontoloji, zooloji ve veteriner hekimlik gibi pek çok bilim alanında kullanılmaya başlanan yeni teknolojiler ve ilerleyen genetik bilimi sayesinde, at türünün kökeni ve evciltme süreci hakkında epey yol katedilmiştir. Yaklaşık altı bin yıl önce Orta Asya'da başladığı düşünülen at evciltme sürecinin ve günümüz evcil at ırklarının kökenleri hakkında yeni bilgiler elde edilmiştir. Yapılan son çalışmalarda atların evciltme bölgeleri ve genetik kökenleri yeniden şekillenmiş, at türlerinin filial yapısı değişmiştir.

1. Introduction

Some phenotypical and genotypical changes are evolved with domestication. It's argued that artificial selection after domestication developed by considering genetic and phenotypic factors, and accordingly, the effect of changes in the gene pool. Trut et al (2009), describe domestication as an evolutionary period that can make selection animals by artificial selection mechanisms, huge phenotypical, behavioural, and psychological changes. Domestication has been accomplished with different areas, and different species at different times. Domestication also affects the human population in some social-economic and techno-economic ways (Price, 2002; Bocquet-Appel, 2008). Phenotypical changes have arisen with some different species, and it is called domestication phenotype (Price, 2002).

Recent studies show the domestication has been made at nine different locations/areas whereas Mesopotamia, China, East United States of America, Andes/ Amazonia, Sahel, Ethiopia, Meso-America, Tropical West Africa and New Guinea. Domesticated animal has spread to other areas with various human and animal movements between regions over time. Various archaeological and paleontological studies from these areas show first domestication movement started about 12.000 years ago (Teletcha, 2019).

Some species have some changes in adult weight and body shape with other morphological changes underline domestication. Some changes are reduced and some of the increase from wild ancestors cause by artificial selection mechanisms in using way of domestication. Exemplary, modern horse breeds are bigger than its ancestor, *eohippus*. Clutton-Brock (1999), state that with domestication animal body getting the short cause of chondrodystrophy; and domestication cause some different head shape (brachiocephalic, mesaticephalic, and dolichocephalic) with reducing nose-neck distance. Other phenotypic changes related to domestication include long and drooping ears, a curly tail, coat colour variations, and fur texture differentiation.

Various evolutionary, and genetic mechanisms have played a direct or alternate role after domestication. As animal species began to be bred under human control, the mechanisms involved in the natural selection process were similarly effective in domestic populations. Similar to the fact that weak animals are selected in nature, individuals with low productivity levels were eliminated from the artificial selection mechanism over time, and their genetic effects were gradually deleted from the population gene pool. It is thought that various variations in yields occur in parallel with the decrease in the pressure of survival in nature after domestication (Price, 2002). Various native breeds can cross that thought but directed selection mechanisms and their effects on the various traits are shores that. As a result, variation, heredity, and selection have preserved continuity like nature after domestication (Jensen and Wright, 2014). How genes were changed completely and their roles in domestication is the most common question, and it's thought that the basic gene controlling several traits may affect the domestication phenotype in different species. With this thought, make another thought like all or some of domestication phenotype traits has developed an adaptive response (Jensen, et al., 2002) Considering all these gene effects, it is seen that the gene actions that are effective in nature continue after domestication.

All the domestication studies argued that with the domestication of horses, humanity began to shape socially and globally. The reason for this is that people start to travel longer distances thanks to horses, many production materials are transported by taking advantage of the horse's gravitational power, and thus trade accelerates. But the most significant point of using horses is started with using them at battle areas. The presence of mounted troops in wars resulted in higher achievements compared to pedestrian armies. Until the industrial revolution, that is, the development of steam vehicles and mechanics, horses have always provided superiority to their owners (Levine, 1999).

However, it is not known exactly from which species and breeds the horses, which have such an important place in the history of domestication, were domesticated. Although previous studies basically mentioned about three different horse breeds, when current molecular techniques examine the remains obtained by various means, it reveals that these three breeds may not be the true origin. The detection of many different maternal lines in haplogroups shaped by similar studies is accepted as an indication that mares are constantly changing in domestication studies and females are easier to obtain than males (Vila et al., 2001; Lindgren et al., 2004).

The aim of this study was evaluate the studies about horse domestication and genetic origin of modern horse breeds.

2. Genetic Mechanism of Domestication

Domestication is a large area for evolutionary, and demographical studies (Zeder 2006). After Darwins's Evolution Theory, many scientists focused on the history of domestication, and the origins of species. Exemplary any study can answer is the domesticated dog from the grey wolf before agricultural period, in one area or different areas (Larson and Fuller, 2014; Larson, 2017). After many years and much genetic innovation, especially using biotechnology, domestication studies have focused and edify on these questions as a multidisciplinary area.

In the first studies on domestication, different breeds belonging to a species; control regions of the mitochondrial genome were amplified and sequenced from different regions and populations. These studies were followed by the creation of various haplotypes and phylogenetic tree cobwebs (Larson, 2011). mDNA shows large variations between species so its use is a great indicator for analyzing demographic enlargement, genetic variation, and phylogenetic texture (Bruford et al., 2003). These sequences are insufficient to describe crossbreeding, and hybridization between different populations, as they only provide amplification of genomes from the maternal line (Larson, 2011). The maternal genome has been widely used in genetic structure studies on cattle (Loftus et al. 1994), pigs (Giuffra et al., 2000) horses (Jansen et al., 2002), and dogs (Verginelli et al., 2005). Substitute the mitochondrial genome, various studies pursuant to the matching of quantitative trait loci (QTL) were conducted in the domestication process of cattle (Khatkar et al., 2004), pigs (Rodriguez et al., 2005), fox (Kukekova et al., 2011), and chickens (Fallahsharoudi et al., 2017), several improvements in genome mapping and origins have occurred. With recent studies, great strides have been made in improving the equine genome map.

In the domestication process, epigenetic factors are also efficient like genetic mechanisms, especially DNA methylation variation causes some differentiation between some species and breeds after domestication has been detected. It is known that epigenetic changes that develop following exposure of individuals to various rearing environments are transmitted to other generations via somatic cells (Guerro-Bosagna et al., 2010; Franklin et al., 2010; Goerlich et al., 2012; Pértille et al., 2017). Despite cell division preserves DNA methylation models, it can sometimes has regulated by an external stimuli (Raynal et al., 2012). Epigenetic factors are thought to play leading role in the development of rapidly evolving phenotypic variations during domestication.

Archaeological and genetic information on the domestication of wild horses (*Equus ferus*) has not fully clarified but various studies are ongoing on this topic. With the observation of a high degree of genetic variation and recurrent mutations in mtDNAs taken from the regions where the first findings of horses were obtained, it becomes increasingly difficult to shape the phylogenetic structure of horses with the results obtained in previous studies (Achilli et al., 2012). Recent studies are gaining momentum to eliminate all these negativities and to define the origin and domestication of the horse (Zhang et al., 2018; Raudsepp et al., 2019; Fages et al., 2019; Vorobieva et al., 2020).

Various studies mentioned mainly three horse breeds as genetic origins of modern horses: the Przewalski horse also knowns as Mongolian wild horse, Equus tarpan, and Equus robustus. Only Przewalski's horse is still alive in the present day (Özbeyaz and Akçapınar, 2021). It is known that among these breeds, Przewalski originated present warm-blooded horse breeds and some cold-blooded horse breeds, while the Tarpan breed was the origin of some European cold-blooded horse breeds. Withal, with the recent genome studies, different breeds can be found in the ancestors of horses; it is suggested that other breeds evolved from two different horse breeds belonging to the Iberian and Siberian regions (Fages et al., 2019).

3. Domestication of Horse

Horses have six key criteria for the domestication of livestock animals (adaptation to changes in feeding regimen, rapid attainment of mature body weight, desire to breed in captivity, docileness, strong psychology, and adaptation to social hierarchy), and it disturbs those horses may have preferred to live close to humans at the beginning of domestication (Diamond, 1997). Domestication of horses is defined as a description of the process of domestication (Cieslak et al., 2010). There are two theories about horse domestication. First of them based on the evidence that horses had different skeletal systems and yields from their ancient ancestors' people bred horses by conscious selection by considering this yields diversity. The second theory is that various organs and tissues of horses such as teeth and bones are used for ornament, weapons, and religious rites by humans. So that is not possible to refer to complete domestication (Ross-Ibarra, 2004).

Considered these theories, a horse domestication model was created; where adult horses are used as a food source, but foals are raised under the control of human. In this case, the needs of the foals are met with their social organization and play skills, and they can be used as food in the following years. At the same time, it was revealed in various excavations and studies that the foals were tried to be raised individually, apart from crowded groups; this situation has brought with it the idea that they behave more closely with people and that their social behaviour skills are shaped under the control of humans. Studies have obtained results that support this domestication theory. Budiansky et al., (1997), suggested that horses in the Western Hemisphere at the end of the Last Glacial Period died out, but domestication prevented the complete extinction of this species due to the protection of horses in Europe and Central Asia. Hausberger et al., (2008) has observed that horses were used as a food source before they used for transport and passenger vehicle in the domestication process. Rollin (2011) claimed that the genetic and physical activities of horses had an important role in the domestication process, but this claim could only capture the traces of recent domestication. It was not possible to determine the gene or genes that started to change between domestic and wild horse breeds. The horses in the cave paintings, which were determined to be made in 4000 BCE, are similar to the Tarpan and Przewalski types. Therewithal, the close interlock between horses and humans is evident in various grave excavations, wall paintings, and jewelry (Larson and Burger, 2013).

The earliest evidence of horse-human interaction has been found in wall paintings in Lascaux Cave in the Dordogne Region of South-eastern France. It is observed that horses are depicted as wild animals in these paintings (Ertuğrul, 2019). When the parietal paintings on the cave walls were examined, it was determined that other game animals were obvious differences in the depictions of horses. When Sauvet (2019), examined the horse figures painted on the cave walls, they found that they were much larger and higher than other species. Also, this study reveals that horse paintings were depicted looking in a different direction from other animals. This situation has brought with it the idea that the horse attracted human attention in the period before it was domesticated and that it had a distinctive feature in their lives. Similarly, under the 2.70 meters horse figure on the ceiling of Rouffignac Cave, other game animals are depicted. The importance attributed to the human of the ancestor cave period has been revealed once again (Ertuğrul 2019).

Archaeological proofs of horse domestication are welded from three sources; i) changes observed of ancient horses' skeleton and teeth, ii) changes in the geographical distribution of ancient horses, especially the spread of horses into areas where there are no wild horses, and iii) archaeological sites containing artifacts, images or evidence of human behaviour associated with horses. Among the archaeological finds are the remains of horses buried in human graves, changes in age and sex of horses killed by them, the complexion of horse pens, bridled and other equipment thought to be used for riding; horses buried with implements intended for the use of horses, such as chariots, and representations of horses used for riding, driving, or pulling, or symbols of manpower. Some of these categories provide irrefutable evidence for domestication in isolation, but the cumulative evidence becomes increasingly compelling. Chariot graves dating to about 2500 BC are the clearest evidence for the use of horses as working animals. Indirect evidence suggests that horses were domesticated long before they were bred around 3500 BC. (Chamberlin, 2006).

The first information about the domestication of horses is encouraged in the Botai Culture which was established on the banks of the Iman-Burluk River in the Northern Kazakhstan region around 3500 BCE, defined as the Copper Age Period. The first link between horses and humans in history was revealed with the discovery of various bones belonging to horses in the 15-hectare area, which was revealed by archaeological studies in 1980 (Mair and Hickman, 2014; Gaunitz et al., 2018). One theory being considered in light of these findings is that the modern horse originated in the Botai culture, where horses were probably bred and milked more than 5000 years ago. A study of ancient and modern horse DNA concluded that modern horses cast in little DNA with Botai horses, but modern horses are not descended from Botai horses. Przewalski and Botai horses appear to be children of another domesticated horse called Borly4 (Gaunitz et al., 2018).

4. Genetic Origins of Domestic Horse

Domesticated stallions and mares can only be analyzed insularly by examining related segments of DNA that are transmitted along the mtDNA or y-DNA. DNA studies suggest that there may be multiple domestication cases for mares, as the several maternal lineages required to explain the genetic diversity of the modern horse suggests that mares are descended from at least 77 different ancestors, divided into 17 different lineages (Jansen et al., 2002). At the same time, genetic evidence of stallion domestication indicates repeated recruitment of wild females to domesticated herds in a single domestication case for a counted of stallions (Vila et al., 2001; Lindgren et al., 2004; Lau et al., 2009). Y chromosome genes are only passed on from ancestor to male cub. These genes infer a far less degree of genetic variation. This suggests that relatively few stallions were domesticated and that many male offspring born from mating between domestic mares and wild stallions are unlikely to be included in the early domesticated breeding line (Lindgren et al., 2004; Lau et al., 2009).

Various analyses of the mtDNA of modern horses, as well as of bones and teeth from archaeological and paleontological finds, show a continuously increasing genetic diversity in the mtDNA. The result of the study shows that a large number of mares are included in the breeding line of the domesticated horse (Vila et al., 2001; Jansen et al., 2002, Cozzi et al., 2004; Cai et al., 2009; Lira, 2010; Priskin et al., 2010). The variation in mitochondrial DNA is used to identify haplogroups (Aksu et al., 2010). The haplogroup is defined as a group of haplotypes that are closely related to each other and share the same common ancestor. Seven main haplogroups (A-G) have been identified in horses, each with several subgroups. Several haplogroups are unevenly distributed worldwide, suggesting the addition of local wild mares to domestic animals (Vila et al., 2001; Jansen et al., 2002; Cai et al., 2009; Priskin et al., 2010; Lira, 2010).

In a 2012 study about genomic sampling of 300 cold-blooded workhorses from territorial areas, previous studies on mtDNA, and y-DNA were reviewed, suggesting that horses were originally domesticated in Eurasian steppe's western part. (Warmuth et al., 2012). Domesticated horses have spread from there. Later, wild mares from local hers were added to domestic herds. Wild mares are thought to be easier to manage than wild stallions. The other parts of world have been excluded from the list of horse domestication for a domestic wild horse population (Lesté-Lasserre, 2015).

DNA sequencing of a 560-780.000-year-old horse in the Yukon region of Canada was using material extracted from the leg bone (Hayden, 2013). Before the study, the oldest successfully sequenced nuclear genome dates back to 110-130 thousand years. For collation, the researchers sequenced a 43,000-year-old Pleistocene horse, five modern horse breeds, a Przewalski horse and a donkey, also. Analysis of the genome differences has proven that the last common progenitor of modern horses, donkeys, and zebras lived between 4 and 4.5 million years ago (Hayden, 2013). It is also revelaled that the Przewalski horse draw apart other modern horse species about 43,000 years ago and was never domesticated in its history (Orlando et al., 2013). A new analysis in 2018 includes genomic sequencing of ancient DNA from the mid-4th millennium BC. Botai domestic horses and domestic horses from many recent archaeological sites and comparing these genomes to those of contemporary domestic horses and Przewalski horses revealed that they not only had similar genetic ancestry to the horses of the Botai culture but were also wild descendants of those horses that had never been domesticated. It was found that the Botai horses made only a negligible genetic contribution to the other ancient or modern domestic horses studied. This supports the idea that they emerged from a distinct domestication that later comprised a separate population of horses. (Pennisi, 2018). The karyotype of the Przewalski's horse differs from that of the domestic horse with an additional pair of chromosomes in that chromosome 5 of the domestic horse divides to give chromosomes 23 and 24 of the Przewalski's horse. In contrast, chromosomal differences between domestic horses and zebras include numerous translocations, fusions, inversions, and centromere shifts (Piras et al., 2009). This is cited as the reason why the Przewalski's horse has the highest diploid chromosome number of any horse breed. It can produce fertile offspring (65 chromosomes) by crossing with a domestic horse (Lau et al., 2009).

Although many studies have been conducted on the origin and domestication mechanisms of present-day's modern horse breeds, these issues have not gained full clarity. Various mtDNA and phylogeny studies have revealed that a large number of females are used in the domestication of horses, and a wide variation is observed within the population, but it has not been determined exactly from which species these females have developed. Various archaeological excavations and paleontological findings suggest that horses undergo many physiological and morphological changes during the domestication process, and this can be achieved by conscious breeding. With the development of various care factors, both epigenetic and direct DNA changes, modern domestic horse breeds are thought to contain a wide genetic variation. It has been revealed in recent studies that Botai horses, which are considered to be the ancestors of modern horses, and Przewalski horses were separated from the modern horse much earlier, but a complete conclusion could not be obtained about the origin of the ancient modern horses, the horses used in the first domestication study. In current studies, it has been put forward that the horse remains found in various excavations and two different horse species that are extinct present-day gather and shaped modern horse breeds. In almost all of the studies, different questions were asked for new research and it was emphasized that the origin studies could be continued with the next generation genome studies.

References

Achiili, A., Olivieri, A., Soares, P., Lancioni, H., Kashani, B.H., Perego, U.A., et al. (2012). Mitochondrial genomes from modern horses reveal the majör haplogroups that underwent domestication. Proc Natl Acad Sci USA., 14;109(7):2449-54. doi: 10.1073/pnas.1111637109.

Aksu, S., Aktopraklıgil, D., Koban, E., Aslan, Ö., Denizci, M., Balcıoğlu, K., et al. (2010). Gen kaynaklarının ve Biyoçeşitliliğin korunması kapsamında yerli at ırklarının genetic karakterizasyonu (Abstract English). BIDAB 3(1): 121-130.

Bocquet-Appel, J.P. (2008). “Explaining the Neolithic demographic transition,” in The Neolithic Demographic Transition And Its Consequences, eds J. P. Bocquet Appel, and O. Bar-Yosef (Dordrecht: Springer), 35–55.

Bruford, M.W, Bradley, D.G., Luikart, G. (2003). DNA markers reveal the complexity of livestock domestication. Nat. Rev. Genet. 4:900. doi: 10.1038/ nrg1203.

Budiansky, S. (1997). The Nature of Horses. New York: Free Press. ISBN 978-0-684-82768-1.

Cai, D., Tang, Z., Han, L., Speller, C.F., Yang, D.Y, Ma, X., et al. (2009). Ancient DNA provides new insights into the origin of the Chinese Domestic Horse. Journal of Archaeological Science, 36 (3): 835-842.

Chamberlin, J.E. (2006). Horse: How the horse has shaped civilization? New York: Blue Bridge. https://archive.org/details/horsehowhorsehas0000cham_n2o8 (Erişim tarihi: 15.02.2021).

Cieslak, M., Pruvost, M., Benecke, N., Hofreiter, M., Morales, A., Reissmann, M., et al. (2010). Origin and history of mitochondrial DNA lineages in domestic horses. PLoS One, 5: e15311. doi: 10.1371/journal.pone.0015311.

Clutton-Brock, J. (1999). A natural history of domesticated mammals. Cambridge University Press, Cambridge.

Cozzi, M.C., Strillacci, M.G., Valiati, P., Bighignoli, B., Cancedd, M., Zanotti, M. (2004). Mitochondrial D-loop sequence variation among Italian horse breeds. Genetics Selection Evolution. 36 (6): 663–672. doi:10.1051/gse:2004023

Diamond, J. (1997).Guns, germs and steel: The fates of human societies. New York: W. W. Norton. ISBN 978-0-393-03891-0.

Ertuğrul, E. (2019). Mağara Resimlerinde Atların Önemi. Arkeofili Online. https://arkeofili.com/magara-resimlerinde-atlarin-ozel-bir-yeri-vardi/.

Fages, A., Hanghoj, K., Khan, N., Gaunitz, C., Seguin-Orlando, A., et al. (2019). Tracking five millennia of horse management with extensive ancient genome time series. Cell, 177: 1419-1435.

Fallahsharoudi, A., de Kock, N., Johnsson, M., Bektic, L., Ubhayasekera, S.J., Bergquist, J., et al. (2017). Genetic and targeted eQTL mapping reveals strong candidate genes modulating the stress response during chicken domestication. G3 (Bethesda). 7 (2): 497-504. doi: 10.1534/g3.116.037721. PMID: 27974436; PMCID: PMC5295596.

Franklin, T.B., Russig, H., Weiss, I.C., Gräff, J., Linder, N., Michalon, A., et al. (2010). Epigenetic transmission of the impact of early stress across generations. BiolPsychiatry. 68(5): 408-15.

Gaunitz, C., Fages, A., Hanghøj, K., Albrechtsen, A., Khan, N., Schubert, M., et al. (2018).Ancient genomes revisit the ancestry of domestic and Przewalski's horses. Science. *360 (6384): 111–114.*

Giuffra, E., Kijas, J., Amarger, V., Carlborg, O., Jeon, J.T., Andersson, L. (2000). The origin of the domestic pig: independent domestication and subsequent intro gression. Genetics 154, 1785–1791.

Goerlich,V.C., Nätt, D., Elfwing, M., Macdonald, B., Jensen, P. (2012). Trans generational effects of early experience on behavioral, hormonal and gene expression response stoacute stress in the precocial chicken. Horm. Behav. 61, 711–718. doi: 10.1016/j.yhbeh.2012.03.006.

Guerrero-Bosagna, C., Settles, M., Lucker, B., Skinner. M.K. (2010). Epigenetic transgenerational actions of vinclozolin on promoter regions of the sperm epiogenome. PlosOne, 5 (9): e13100.

Hausberger, M., Roche, H., Henry, S., Visser, E.K. (2008). A review of the human–horse relationship. *Appl.* Anim. Behav. Sci. 109, 1–24.

Hayden, E.C. (2013). "First horses arose 4 million years ago". Nature. doi:10.1038/nature.2013.13261.

Jansen, T., Forster, P., Levine, M.A., Oelke, H., Hurles, M., Renfrew, C., et al. (2002)."Mitochondrial DNA and the origins of the domestic horse". Proceedings of the National Academy of Sciences. 99 (16): 10905–10910. Bibcode:2002PNAS...9910905J. doi:10.1073/pnas.152330099. PMC 125071. PMID 12130666.

Jensen, P., Wrigt, D. (2014). Behavioral Genetics and Animal Domestication, in Genetics and the Behavior of Domestic Animals. Chapter II, 41-80. Ed. Gonzalez P. Elsevier.

Khatkar, M.S., Thomson, P.C., Tammen, I., Raadsma, H.W. (2004). Quantitative trait loci mapping in dairy cattle: review and meta-analysis. Genet. Select. Evol. 36:163. doi: 10.1186/1297-9686-36-2-163.

Kukekova, A.V., Trut, L.N., Chase, K., Kharlamova, A.V., Johnson, J.L., Temnykh, S.Y., et al. (2011). Mapping loci for fox domestication: deconstruction / reconstruction of a behavioral phenotype. Behav. Genet. 41, 593–606. doi: 10.1007/s10519-010-9418-1.

Larson, G. (2011). Genetics and domestication: important questions for new answers. Curr. Anthropol. 52: 485–495.

Larson, G. (2017). Reconsidering the distribution of gray wolves. Zool. Res. 38: 115. doi: 10.24272/j.issn.2095-8137.2017.021.

Larson, G., Burger, J. (2013). A population genetics view of animal domestication. Trends Genet. 29: 197–205. doi: 10.1016/j.tig.2013.01.003.

Larson, G., Fuller, D.Q. (2014). The evolution of animal domestication. Ann. Rev. Ecol. Evol. Syst. 45: 115–136.

Lau, A.N., Peng, L., Goto, H., Chemnick, L., Ryder, O.A., Makova, K.D. (2009).Horse domestication and conservation genetics of

Przewalski's Horse in ferred from sex chromosomal and autosomal sequences. Molecular Biology and Evolution. 26 (1): 199–208. doi:10.1093/molbev/msn239. PMID 18931383.

Lesté-Lasserre, C. (2015). Excitement, feeling and attachment's impact on training. The Horse. https://thehorse.com/116463/excitement-feeling-and-attachments-impact-on-training/ (Erişim tarihi: 20.05.2021).

Levine, M.A. (1999). Botai and the origins of the horse domestication. Journal of Antrhopological Archeology. 18: 29-78.

Lindgren, G.N., Backström, J., Swinburne, L., Hellborg, A., Einarsson, K., Sandberg, G., et al. (2004). Limited number of patrilines in horse domestication. Nat. Genet. 36: 335-336.

Lira, J., Linderholm, A., Olaria, C., Brandstro, M., Durling, M., Gilbert, M.T.P., et al. (2010) Ancient DNA reveals traces of Iberian Neolithic and Bronze Age lineages in modern Iberian horses. Molecular Ecology 19: 64–78.

Loftus, R.T., Machugh, D.E., Bradley, D.G., Sharp, P.M., Cunningham, P. (1994). Evidence for two independent domestications of cattle. Proc. Natl. Acad. Sci. U.S.A. 91, 2757–2761. doi: 10.1073/pnas.91.7.2757.

Mair, V.H., Hickman, J. (2014). Reconfiguiring the Silk Road: New research on East-West Exchange in antiquity. University of Pennsylvania Press. P. 15. ISBN: 978-1934536698.

Orlando, L., Ginolhac, A., Zhang, G., Froese, D., Albrechtsen, A., Stiller, M., et al. (2013). "Recalibrating Equus evolution using the genome sequence of an early Middle Pleistocene horse". Nature. 499 (7456): 74–8.Bibcode:2013Natur.499...74O. doi:10.1038/nature12323. PMID 23803765. S2CID 4318227.

Özbeyaz, C., Akçapınar, H. (2021). Hayvan Yetiştiriciliği (Temel Bilgiler). Medisan Yayınları, Ankara.

Pennisi, E. (2018). "Ancient DNA up ends the horse family tree". sciencemag.org. (Erişim tarihi: 24.05.2021).

Pértille, F., Brantsaeter, M., Nordgreen, J., Coutinho, L.L., Janczak, A.M., Jensen, P., et al. (2017). DNA methylation profiles in red blood cells of adult hens correlate with the irrearing conditions. J. Exp. Biol. 220, 3579–3587. doi: 10.1242/jeb.157891.

Piras, F.M., Nergadze, S.G., Poletto, V., Cerutti, F., Ryder, O.A., Leeb, T., et al. (2009). Phylogeny of horse chromosome 5q in the genus Equus and centromere repositioning. Cytogenetic and Genome Research. 126 (1–2): 165–172. doi:10.1159/000245916. PMID 20016166. S2CID 24884868.

Price, E.O. (2002). Animal Domestication and Behavior. Wallingford: CABI.

Priskin, K., Szabo, K., Tomory, G., Bogacsi-Szabo, E., Csanyi, B., Eordogh, R., et al. (2010). Mitochondrial sequence variation in ancient horses from the Carpathian Basin and possible modern relatives. Genetica. 138 (2): 211–218. doi:10.1007/s10709-009-9411-x. PMID 19789983. S2CID 578727.

Raudsepp, T., Finno, C.J., Bellone, R.R., Petersen, J.L. (2019). Ten years of the horse reference genome: insights into equine biology, domestication and population dynamics in the post-genome era. Anim Genet. 50(6):569-597. doi: 10.1111/age.12857. Epub 2019 Sep 30. PMID: 31568563; PMCID: PMC6825885.

Raynal, Nj.M., Si, J., Taby, R.F., Gharibyan, V., Ahmed, S., Jelinek, J., *et al.* (2012). DNA methylationdoes not stablylock gene expression but instead serves as a molecular mark for gene silencing memory. Cancer Res. 72, 1170–1181. doi: 10.1158/0008-5472.CAN-11-3248.

Rodriguez, C., Tomas, A., Alves, E., Ramirez, O., Arque, M., Munoz, G., *et al.* (2005). QTL mapping for teat number in an Iberian-by-Meishanpiginter cross. Anim. Genet. 36, 490–496. doi: 10.1111/j.1365-2052.2005.01358.x

Rollin, B. (2011). Putting the horse before Descartes: My Life's Work On Behalf Of

Animals. Philadelphia: Temple University Press.

Ross-Ibarra, J. (2004). The evolution of recombination under domestication: a test of two hypotheses. Am. Nat. 163, 105–112. doi: 10.1086/380606.

Sauvet, G. (2019). The Hierarchy of Animals in the Paleolithic Iconography. Journal of Archeological Science: Reports, 28, 102025.

Teletchea, F. (2019). Animal Domestication: A Brief Overview. Animal Domestication, Intech Open.

Trut, L., Oskina, I., Kharlamova, A. (2009). Animal evolution during domestication: The domesticated fox as a model. Bioessays 31: 349-360.

Verginelli, F., Capelli, C., Coia, V., Musiani, M., Falchetti, M., Ottini, L., et al. (2005). Mitochondrial DNA from prehistoric canids highlights relationships between dogs and South-East European wolves. Mol. Biol. Evol. 22, 2541–2551. doi: 10.1093/molbev/msi248.

Vilà, C., Leonard, J.A., Götherström, A., Marklund, S., Sandberg, K., Lidén, K., et al. (2001). Wide spread origins of domestic horse lineages. Science 291: 474–477. doi: 10.1126/science.291.5503.474.

Vorobieva, N.V., Makunin, A.I., Druzhkova, A.S., Kusliy, M.A., Trifonov, V.A., Popova, K.O., et al. (2020) High genetic diversity of ancient horses from the Ukok Plateau. PLoS ONE 15(11): e0241997. https://doi.org/10.1371/journal.pone.0241997.

Warmuth, V., Eriksson, A., Bower, M., Barker, G., Barrett, E., Hanks, B., et al. (2012). Reconstructing the origin and spread of horse domestication in the Eurasian steppe. Proceedings of theNational Academy of Sciences of the United States of America, 109 (21): 8202-8206.

Zeder, M.A. (2006). Central questions in the domestication of plants and animals. Evolutionary Anthropology. 15:105-117.

Zhang, C., Ni, P., Ahmad, H.I., Gemingguli, M., Baizilaitibei, A., Gulibaheti, D., *et al.* (2018). Detecting the population structure and scanning for signatures of selection in horses (Equus caballus) from whole-genome sequencing data. Evol. Bioinform. 14:1176934318775106. doi: 10.1177/1176934318 775106.