

ON THE ORIGIN OF MODERN HORSE BREEDS FROM FOUR DISTINCT SUBSPECIES
OF *EQUUS CABALLUS*

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ABSTRACT

Although the evolution and domestication of the horse has been extensively studied, many mysteries remain. No other animal has been as influential on the development of human societies and cultures as the horse. Horses have been used for milk, meat transportation, riding, plowing, transportation of goods, and recreation. Over the course of the domestication of the horse, specific traits were selected for or against depending on the intended use of the animal. A variety of types of horses appeared in different regions of the world and it has been theorized that several indigenous subspecies of wild horses were used to create the modern domestic breeds that we know today. This paper provides evidence that four subspecies are the forerunners to today's horse.

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DEDICATION

This paper is dedicated to my Swedish grandmother, Margaret Louise Abrahamson Carlson, who encouraged me to study horses.

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GENERAL INTRODUCTION

Evidence suggests that domestic horse breeds have arisen from four wild subspecies of horses from around the world. In this paper I provide evidence that these distinct subspecies have contributed to variation in morphological and physiological traits of modern breeds and that historical traits are preserved in distinct breeds from evidence based on genetics and morphological features. My hypothesis is that the evolution of modern horse breeds arose from the selective breeding of these four distinct subspecies of wild horses through selection and domestication by humans.

In the 1700s, taxonomy and classification was accomplished through the study of morphological comparisons, habitats, locations, and lifestyles of different animals. We now have the ability to conduct DNA analysis to assess the relationships among species. In this paper I have compared the process of speciation through natural selection and artificial selection. I have purposefully researched references from very early studies on horse domestication. Even though these studies did not have the ability to test DNA, the fact that there was little admixture of breeds 100 years ago and that there were fewer breeds at the time was useful in understanding the historical aspect of taxonomic classification of horse subspecies.

The designation of “species” vs. “subspecies” is partly a question of semantics, but it is assumed that the classification hierarchy identifies the most likely evolutionary history of an organism. It should be noted that many specific and subspecific names have been given to both extant and extinct members of the genus *Equus* (Bennett and Hoffman, 1999). These names and their assignments have been the subject of much debate. I argue that we can also include “variety,” “type,” “race,” or “breed” to this list of descriptive terms when considering domestic animals. This paper will expand on the history of artificial selection in relation to the evolution

of domestic horse breeds. The evolution of the horse is one of the most documented and studied examples due to the extensive fossil record.

Several horse subspecies were the ancestors of what we refer to as the modern domestic horse, *Equus caballus* (Ewart, 1904; Ridgeway, 1905; Lydekker, 1912; Speed and Etherington, 1952a; Speed and Etherington, 1952b; Speed and Etherington, 1953; Benett and Hoffman, 1999; Gonzaga, 2004). Over the course of domestication, specific traits were selected in response to the horses' use intended by humans. Breeds were created, modified, interbred, went extinct, and new ones created all under the influence of breeders selecting for very specific characteristics.

SECTION I: GENERAL LITERATURE REVIEW

The delineation of what constitutes a species and the process of speciation are not fundamentally different between wild and domestic species. Historically, we assign names for species of domestic animals differently than that of wild animals. For example, wild species populations have subspecies whereas domestic species are classified into breeds. Species of wild animals are formed by natural selection and breeds of domestic animals are formed by artificial selection. Species are defined as populations that are reproductively isolated from others and occupy a specific niche in nature. However, we have many examples of wild animals that interbreed with domesticated ones. Does this change our concept of species? For example, in domestic cats, *Felis catus*, a new breed of cat has been created by breeding Asian Leopard cats (*Prionailurus bengalensis*) with domestic cats, which results in a breed called the Bengal, with the species name of *Felis lybicus*. This newly designated species is a domestic pet, and provides an example of the difficulty in understanding the application of taxonomic classification to domestic plants and animals. This review will focus on current biological terminology and taxonomy as it relates to evolution.

Species

The formation of species in nature occurs by evolution and adaptation to selective environmental pressures. Bush (1975) explains modes of speciation and argues against the idea that speciation only occurs allopatrically, after a population becomes isolated from its parent group causing reduced genetic diversity. He explains other types of speciation: parapatric and sympatric. Parapatric speciation occurs when individuals of one species invade a neighboring environment and evolve characteristics better suited to that new niche (Bush, 1975). In

sympatric speciation, reproductive isolation arises before a species invades a new niche (Bush, 1975).

The biological species concept described by Mayr in 1942 states, “A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.” An example would be populations of animals restricted to islands. In Section II we provide the example of the Exmoor pony that was isolated on the British Isles before domestication events took place. Domestic animal breeds are similarly isolated from each other, albeit by man, and occupy a specific niche, or role, in society. For example, once horses were domesticated, they did not return to the wild to breed but remained in captive breeding programs with traits artificially selected for or against by humans.

The evolutionary species concept of mammalian paleontologist George Gaylord Simpson in its modern form defines species as “a single lineage of ancestor-descendant populations that maintains its identity from other such lineages and that has its own evolutionary tendencies and historical fate” (Simpson, 1951).

The Modern Synthesis unifies Mendelian genetics and Darwin’s theory of evolution. The study of both genetic relationships and morphological similarities and differences among taxa are pertinent to classification. The ability to study DNA and mitochondrial DNA (mtDNA) has revolutionized taxonomy and classification. Scientists are able to analyze familial DNA and piece together the evolutionary events that resulted in different species. This has been instrumental in the study of both convergent and divergent evolution.

Convergent evolution is defined by traits that have evolved independently to similar function or morphology due to existence in similar environments. One example is the thylacine, or Tasmanian wolf, also called Tasmanian tiger (*Thylacinus cynocephalus*), now believed to be

extinct. This was a marsupial carnivore that resembled a large canine and occupied a similar niche in its native Australia. The marsupial thylacine, as wolf-like as it appeared, was not at all related to the placental wolf of either Europe or North America. The closest relative to the thylacine is the Tasmanian devil (*Sarcophilus harrisi*), another carnivorous marsupial.

In divergent evolution, however, different species can be traced back to a single common ancestor. Through this process, populations evolved along different evolutionary paths resulting in the formation of new species. This is what has taken place in the Equidae family as all the extant species including asses, zebras, onagers, and horses are believed to have diverged from a single common ancestor 1.9-2.3 million years ago (Yang *et al.*, 2003). Evolution is defined as a change in allele frequency in a population over time that resulted in different species due to their diverse environmental pressures and reproductive success. Within the different Equidae species, the appearance of subspecies is the result of smaller populations isolated from others. The subspecies populations, due to a smaller gene pool, will develop distinct characteristics of their own, yet are still able to breed with individuals of other subspecies and produce viable and fertile offspring.

Two types of speciation are demonstrated in the evolution of the domestic horse. First, allopatric speciation occurs when there is isolation between populations and then subsequent time for genetic drift, such as seen in the Icelandic horse. In this example, the Vikings brought horses to Iceland in about 900 AD where they were isolated for 1,000 years. Allopatric speciation often involves inbreeding and can result in the fixation of homozygous traits (Bush, 1975). Human habitat manipulation and sexual selection allows domestic breeds to remain in an allopatric process in order to avoid outcrossing between breeds (Tiemann and Rehkämper, 2012). Second, sympatric speciation occurs when a new species forms directly from the parent species

with “pre-mating reproductive isolation” taking place before the population moves to a new environment (Bush, 1975). An example of this is the formation of the modern horse breeds during domestication. Animals that were able to be caught, tamed, and trained for tasks would be selected for breeding with others with the same characteristics moving out of the natural environment and into the domesticated world. In other words, both allopatry and sympatry have taken place in the domestication process of the horse.

Interspecific Breeding

One criterion generally accepted to distinguish different species is that no viable offspring result from their hybridization. Therefore, it is somewhat surprising to find hybridization occurring between wild taxa. This would be easily accomplished by the predecessors to the domestic horse if the regions between subspecies overlapped. Even after establishing the criteria for classification of species, we have discovered situations where separate species have hybridized.

In 1965, a study of two zebra species coexisting in an overlap zone in Kenya found that hybrids between Grévy’s zebra (*Equus grévyi*) and Burchell’s zebra (*Equus burchelli*) did not occur (Keast, 1965). Grévy’s zebra is the larger of the two species, has thin, narrow stripes that do not meet under the belly and has large, rounded ears. Burchell’s zebra has broad stripes that meet under the belly and the ears are smaller and pointed. However, in 2009, in this same zone, Cordingley *et al.* reported that hybridization between the endangered Grévy’s zebra and Burchell’s zebra was taking place. It appears that the Grévy’s zebra is disappearing due to matriculation of its genes into the Burchell’s species.

Interestingly, Grévy’s zebra has a diploid chromosome number of 46, Burchell’s has $2n = 44$, and in captivity hybrid offspring have been found to have $2n = 45$ (Cordingley *et al.*, 2009).

The resulting hybrid females are fertile and appear to be incorporated into the Burchell's zebra herd. Interestingly, all hybrid females are the result of Grévy males mating to Burchell's females. The male hybrids by Grévy males out of Burchell's females were believed to be infertile due to the lack of observance of foals that would have been produced by them after observed matings of these hybrid males with the females in their herd (Cordingley *et al.*, 2009). Since these males were born into and raised in the Burchell herd, they were only observed mating with Burchell's females (Cordingley *et al.*, 2009). This male sterility is an example of Haldane's Rule, which states "When in the F₁ offspring of a cross between two animal species or races one sex is absent, rare, or sterile, that sex is always the heterozygous sex." (Haldane, 1922; Forsdyke, 2000). The mechanism for this is due to an asynapsis of homologous chromosomes during meiosis (Bhattacharyya *et al.*, 2013). There was no evidence of the reciprocal cross of Burchell's males to Grévy's females. In this same region of Kenya, hybridization has been observed between different ungulate species, the Somali reticulated giraffe (*Giraffa camelopardalis reticulata*) and the Masai giraffe (*Giraffa capensis tippelskirchi*), considered to be two distinct species both in terms of phenotype and habitat preference (Stott, 1959). According to Gray (1971), all of the species and subspecies of *Giraffa* can interbreed and in 2007, Brown *et al.* proposed that the current subspecies divisions of *Giraffa* be reclassified at the species level due to their phenotypic diversity and the fact that they are reproductively isolated due to geographic separation.

The Brahma and Angus cattle, are both domestic breeds, and are classified as two different species, *Bos indicus* and *Bos taurus*, respectively. Both species have the same number of diploid chromosomes of $2n = 60$, and can readily interbreed and produce viable offspring. This has resulted in the formation of a separate breed: the Brangus. A major phenotypic difference is that

Bos indicus is humped and *Bos taurus* is humpless. These two species resulted from separate domestication events and separate ancestors resulting in some differences in distribution of alleles (MacHugh *et al.*, 1997). However, these allelic differences have no effect on fertility and there is currently much debate on the classification of these species as breeds, subspecies, or one species (Buchanan, personal communication).

Interspecific matings are readily observed both in nature and under domestication. In the case of the horse, wild subspecies from around the world were able to mate with other subspecies given the right conditions. It would not be unfounded to suggest that the extinction of the domestic horse predecessors was due to introgression into already domesticated horses. As characteristics are selected for or against in a breeding program, certain traits can be lost as selection continues. By continuing to breed on type or subspecies into another, the original characteristics of those subspecies would become intermingled and new subspecies would form at the expense of losing the ancestral population.

Darwin And Theories Of Evolution

Evolution is defined as: “changes in the heritable traits of a population of organisms as successive generations replace one another,” (National Academy of Sciences, 2009). It is populations of organisms that evolve, not individual organisms. The evolution of the horse has been studied extensively, yet the exact history remains a mystery (Eisenmann and Turlot, 1978; Eisenmann, 2004). The first horses, or rather the ancestral horse, also known as *Eohippus*, appeared in both Europe and North America 58 million years ago during the early Eocene epoch (MacFadden, 1992). Horse evolution to include the appearance of several genera and species along with multiple crossings over both the North Atlantic route and the Bering land bridge into Eurasia took place until the late Pleistocene epoch (Forsten, 1989; MacFadden, 1992).

Approximately 11,000 years ago, all horses became extinct in North America during the late Pleistocene/early Holocene epochs (Simpson, 1961; Forsten, 1989; MacFadden, 1992; Kefena *et al.* 2011). The fact that horses were indigenous to North America, albeit many years ago, has scientists today arguing that the feral mustang of America's West is simply a reintroduction of a species to their original habitat (Kirkpatrick and Fazio, 2010). By understanding the theories of evolution, we can build a better picture of the development of the horse through time. Although most people think of evolution as the study of fossils, animal populations are continuing to evolve even today. Natural selection, the changes that occur in a population of a species as a result of the environment, is the driving force behind the evolution of populations of wild animals. Artificial selection, the changes that occur in a captive population of a species as a result of human breeders, is the driving force behind the evolution of populations of domestic animals.

There are several theories of evolution dating back to the late 1700s. The main ones that biologists have concerned themselves with are that of Jean Baptiste de Lamarck and Charles Darwin. Lamarck, wrote the *Philosophie Zoologique* in 1809 where he described the spontaneous generation of traits. In other words, characteristics needed by the parents in their environment would spontaneously be inherited by their offspring in order that the offspring derive increased fitness to survive and reproduce in their environment. A good example of the logic used in this theory is that of the giraffe that originally had a relatively short neck and with the need to stretch the neck to lengthen and reach the better food source, higher leaves, the offspring of this giraffe would be born with a longer neck. This theory came to be referred to as Lamarckism. Although this theory is not currently accepted, it is mentioned here as an example of one of the previous explanations of evolution.

During this same era of biological and zoological exploration and interpretation, Charles Darwin wrote about natural selection and the theory of evolution in his famous work *On the Origin of Species* (Darwin, 1859). Darwin was also an avid breeder of domestic pigeons and referred to breeding of domestic animals as artificial selection (Darwin, 1868). Here, breeders, not environmental changes or pressures, social structure, or sexual selection by the animal, are the driving force behind the changes and formation of domestic species (Richards, 1998). Darwin contemplated the changes in species and discussed whether these were abrupt events or changes that appeared over time (Wright, 1978).

Darwin stated that both natural and artificial selection were similar processes since they were both capable of great change (Richards, 1998). Darwin's contemporaries argued that species under domestication were immutable and that Darwin's analogy was unfounded, despite that change resulting from artificial selection rendered an inability to return individuals to the original species form (Richards, 1998). However, Darwin himself agreed that natural selection results in fitness of a species, and artificial selection does not. The definition of fitness is the ability of an individual to survive in its environment and produce fertile offspring capable of reproducing. In the wild, fitness of an individual is crucial. In domestic animals, fitness as defined above is not necessary as the domestication process has rendered individual animals dependent upon humans for their survival and reproduction. For domestic animals and plants, fitness is a property of an individual possessing the capacity to survive and to reproduce viable offspring that continue to exhibit these traits in a captive environment.

Darwin viewed artificial selection as an experiment and because domesticated individuals do not necessarily have the context of increased fitness, fitness being a product of both survival and successful reproduction of fertile offspring in the wild, the generation of new species would

be unlikely (Richards, 1998). However, although wild species would not necessarily form, artificial selection could create domestic species. Darwin believed that artificial selection would accelerate the evolutionary process and that appreciation of the capacity of artificial selection was essential to understanding natural selection (Driscoll *et al.*, 2009). Edward O. Price (2008) supported the theory of evolution by comparing wild and domestic phenotypes and their relationship with humans. The selection of new traits that breeders find appealing is in contrast to natural selection (Price, 2008). This is due to the domestication process and the characteristics that the breeder finds appealing as opposed to what is necessary for that individual to survive in a natural environment. The breeder in artificial selection accomplishes the simulation of natural selection because the breeder makes conscious choices as opposed to a non-directed process that occurs in nature (Rice and Hostert, 1993). This goes back to Darwin's statement of how the breeder takes on the role of sexual selection by mate choice (Darwin, 1872).

George Wallace argued against the analogy that artificial selection was simply natural selection driven by the breeder, due to the inability of artificial selection to render fitness in the wild (Richards, 1998). He refers to domestic pigs, sheep, pigeons and poodles as examples of animals that would be unable to exist in nature (Richards, 1998). These breeds have been created by selection of traits beneficial to humans. Trait selection in domestic animals results in higher fitness of particular animals that provide a benefit for human society (e.g., higher crop production, or particular coat colors), as opposed to a free-living organism whose phenotypes result in higher survival and reproduction under sometimes-difficult conditions. In domestic animal breeding, selection is for the traits that are considered to be useful and fit for human needs. Many of our modern domestic animals would not be able to survive in the wild environment, even if returned to an environment in which their ancestors originated. Natural

selection and artificial selection are both based on new traits that appear by chance. The difference is that breeders have a different goal in choosing for or against these new traits as opposed to which traits would result in individuals with higher fitness in nature (Tiemann and Rehkämper, 2012). However, because domestic species do not live in the wild, they have indeed fulfilled an unoccupied niche on the farm (Rubin *et al.*, 2010).

Domestication

Herre and Röhrs (1990) studied domestication research and believed domestication to be a model of evolution. Their results concluded that domestication does not lead to new species, due to the fact that breeding between domestic animals and their wild relations would still exist. This is true in that there are many examples of domestic species who are fully capable of breeding and producing viable and fertile offspring when crossed with their wild species relative: dog – wolf, domestic cat – serval, domestic cattle – bison, domestic horse -Przewalski's horse. Even with this ability, taxonomists have assigned different species names to the wild and domestic counterparts.

Tiemann and Rehkämper (2012) state that they see domestication as an evolutionary process. In birds, mate choice is important and female choice of males drives sexual selection (Tiemann and Rehkämper, 2012). In their 2012 study, Tiemann and Rehkämper used White Crested Polish (WCP), Red Leghorn, and Lohmann Leghorn Classic chickens to test for assortative mating in a freely interbreeding population. If the breeds of chickens were to choose mates of like kind, the Biological Species Concept would be supported. Their results did indicate a preference of WCP hens for WCP cocks in mating supporting the argument of the formation of new species within domestic taxa (Tiemann and Rehkämper, 2012). Their studies implied that it is possible for new species to form, even in domestic animals.

The domestication process changes selection to that of the breeder as opposed to environmental pressures driving natural selection. Evolution is apparent as populations of the original species gain or lose characteristics through diversification and breeder selection. Artificial selection by the breeder involves prezygotic selection (choosing the parents) as opposed to postzygotic selection which is found in natural selection (Driscoll *et al.*, 2009). They also referred to weak (passive selection with the breeder not actively involved) vs. strong (active selection by the breeder) artificial selection in either prezygotic or postzygotic selection. This is selection of desirable traits that would then limit the genes available in a population. An example of weak selection would be the non-selective breeding of domestic donkeys seen in African nomadic cultures where unmanaged breeding of a domestic herd allows interbreeding with wild donkeys (Marshall *et al.*, 2014).

In strong artificial selection, an example of prezygotic selection would be individually selecting parents for mating, as in domestic breeding. An example of strong artificial postzygotic selection would be removing from the breeding program any individuals that did not meet the expectations of the prezygotic selection. The breeding of domestic horses follows strong prezygotic and postzygotic selection. Genetic analysis of mtDNA has provided evidence that very few stallions were used with many mares in the domestication process (Levine, 1999; Kavar and Dovic, 2008; Lau *et al.*, 2009; Cieslak *et al.*, 2010; Groeneveld *et al.*, 2010). The fact that very few stallions were used indicates strong postzygotic selection as only stallions that met the criteria set forth were kept and used for breeding. The stallion is a good example of postzygotic selection as stallions are difficult to keep in a domestic setting with many mares and other stallions present. Therefore, choosing desirable traits is pertinent to the success of the breeding program. In domestic species, success can be defined as the production of animals that meet the

standard set forth by the breeding guidelines for that particular breed. In draft horses, strength and ability to work in a team would be selected over speed and jumping ability, for example. Prezygotic choices of breeding individuals is made and after the offspring is evaluated, either in the field, or under selective judgment according to a predefined standard, postzygotic selection can be made to either remove an individual from the breeding program or recommend it to continue developing specific traits. Strong prezygotic selection in choosing breeding animals that would meet the needs of the humans was essential during the domestication of the horse. The horse was originally domesticated for meat, milk, and transportation and it was not until humans realized that horses were more efficient than the ox for plowing that horses were put to harness (Clutton-Brock, 1999). Depending on the environment and location, humans used the types of horses available to them.

Domestication Of The Horse

The earliest evidence of horse domestication dates to 9400 B.C. (Jansen *et al.*, 2002). The horse, while most likely domesticated for meat, is currently the subject of much debate as to when it was first used as a riding animal (Levine, 1998; Gonzaga, 2004; Kavar and Dovc, 2008). There are two main theories that differ as to method and location of domestication events. One theory is that the wild horses of Mongolia, *E. przewalksii*, were captured along with their foals, selected for tameness, and then those foals were reared by humans (Levine, 1998). Selective breeding for tameness and tractability would have led to domestication (Levine, 1998).

The second, and most commonly accepted theory, is the occurrence of a series of separate events that resulted in domestication of the Tarpan, *Equus ferus ferus*, also referred to as *Equus ferus gmelini*, in Western Europe, and the Eurasian steppe (Downs, 1961; Forsten, 1989; Spassov and Iliev, 1997; Lister *et al.*, 1998; Bowling and Ruvinsky, 2000; Vilà *et al.*, 2001; Jansen *et al.*,

2002; Gonzaga, 2004; Cieslak *et al.*, 2010; Kefena *et al.*, 2011, Warmuth *et al.*, 2011). The Tarpan was first described by German naturalist Gmelin in 1769 in Russia, near Voronzeh, and became extinct in 1909. Although it cannot be tested, due to the lack of available DNA, there is a widely held belief that the Tarpan had 64 chromosomes giving it credence as the ancestor of the modern horse, *Equus caballus*, which also has a diploid number of chromosomes of 64 (Bennett and Hoffman, 1999). This is in contrast to Przewalski's horse that has a diploid number of 66 chromosomes.

Although the Tarpan is given credit as the ancestor of all the domestic breeds, the lack of any DNA evidence cannot support this completely. Several authorities studying the evolution of the domestic horse have questioned its validity and relegated it to a mixture of breeds (Ridgeway, 1905; Lydekker, 1912; Speed, 1953). Speed (1953) states that the Tarpan "probably never existed as a real entity." This was previously questioned in 1884 due to there being no family history and only one drawing of a living animal (Speed, 1953). According to Speed, there were no records of parentage, no purebred progeny, and there was no conformation to a distinct type, either extant or extinct (Speed, 1953). Many sources state that there is an absence of any skeletal remains or even photographs. However, Clutton-Bruck (1999) refers to a skull and skeleton housed at the Soviet Academy of Sciences in St. Petersburg, Russia and Lydekker (1912) provides a photo (Fig.1) and states that a skeleton is in the Zoological Museum in Moscow. Verification of skeletal remains is needed. The last known Tarpan in existence died in 1909 at the Moscow Zoo and was stated to be a cross of a Tarpan with a domestic horse. The difficulty in finding concrete evidence of the Tarpan's existence and role in horse domestication is perplexing. Further study of the elusive Tarpan is certainly warranted.



Fig. 1: Tarpan mare.
Photo from *The Horse and Its Relatives* by R. Lydekker, 1912.



Fig. 2: Przewalski's horses in their natural habitat in Mongolia in 2013.
Photos by Kate Jenks PhD.

Przewalski's horse (Fig. 2), *Equus przewalskii*, was first discovered in 1879 by the Russian explorer, Colonel N. M. Przewalski, in Mongolia. These animals have been determined to be the last remaining wild horse, and, although extinct in the wild since 1966, they have now been reintroduced into wildlife preserves in Mongolia. *E. przewalskii* is designated as a separate species due to having a karyotype of 66 chromosomes in contrast to the 64 chromosomes found

in *E. caballus* (Benirschke et al., 1965; Bowling and Ruvinsky, 2000; Groves and Ryder, 2000; Myka et al., 2003). Despite this difference, *E. przewalskii* and *E. caballus* are two equines capable of interspecific reproduction resulting in fertile offspring (Benirschke et al., 1965; Short et al., 1974). These hybrid offspring often exhibit polymorphism in having 65 chromosomes (Short et al., 1974). Although many of the equines (horses, asses, zebras) can hybridize and create viable offspring, the only other equines able to produce fully fertile offspring from an interspecific mating are the wild African ass, *Equus africanus*, when crossed with the domestic donkey (*Equus asinus*). However, it should be noted that both of these species have a diploid chromosome number of $2n = 62$ (Allen and Short, 1997; Clutton-Brock, 1999; Marshall et al., 2014).

Different theories exist as to the occurrence of the karyotype of *E. caballus*. One theory is that the ancestor of the Tarpan or the Tarpan itself had 66 chromosomes, same as *E. przewalskii*, but that a Robertsonian translocation (centric fusion) replaced four acrocentric chromosomes with two metacentric chromosomes, resulting in an animal with 64 chromosomes (Short et al., 1974; Bowling and Ruvinsky, 2000, Groves and Ryder, 2000; Myka et al., 2003). In crosses between *E. caballus* and *E. przewalskii* it has been established that Robertsonian translocation does take place and the F1 progeny have either 64 or 65 chromosomes. (Short et al., 1974). Since hybrids between *E. przewalski* and *E. caballus* are fertile (Koulischer and Frechkop, 1966), it could be that these hybrids formed new subspecies and then breeds. Also, although the F1 hybrids had 65 chromosomes, the F2 generations appeared with 64 (Koulischer and Frechkop, 1966). Meanwhile, the possibility exists that the ancestor of all horses possessed 64 chromosomes and that a chromosomal change such as a fission event increased the chromosome number to 66 (Ishida et al., 1995).

The appearance of a variety of coat colors and patterns in horses is believed to be the result of domestication. Wild taxa are homogenous with respect to coat color, domestic taxa have been bred to exhibit a large range of coat colors. By testing the bones of wild horses from the Late Pleistocene and early Holocene, the ancestral coat color in the horse was determined to be bay or bay dun, the color found in the Przewalski's horse (Ludwig *et al.*, 2009). The Exmoor pony is uniformly bay with no white markings indicating wild type appearance (Baker, 2008). The changes in coat colors in the horse to include black, chestnut, tobiano, sabino, buckskin, and black silver appeared during the Bronze and Iron Ages (Ludwig *et al.*, 2009). This coincides with the domestication events of the horse. Interestingly, however, recent studies determined that changes in coat color and pattern, to include spotting, actually occurred during prehistoric times which coincide with Paleolithic cave paintings, giving credence to the authenticity of the artist portraying the existing horses (Gonzaga, 2004; Pruvost *et al.*, 2011). See Table 2.

Stallions

Analysis of the Y chromosome of *E. przewalskii* revealed two haplotypes, both in common with the lineage of the zebras, asses, and onagers (Wallner *et al.*, 2003). Also, mitochondrial DNA (mtDNA) studies show marked overlap in the sequence variation between *E. przewalskii* and *E. caballus* which does not support the hypothesis that *E. przewalskii* is an example of the ancestral state (Wallner *et al.*, 2003; Kefena *et al.*, 2011) but rather a relative (Groves and Ryder, 2000; Lindgren *et al.*, 2004; Der Sarkissian *et al.*, 2015).

In contrast to *E. przewalskii*, the presence of a single Y chromosome haplotype in *E. caballus* (Kavar *et al.*, 2002; Lindgren *et al.*, 2004; Wallner *et al.*, 2004) indicates that domestication of the horse involved few stallions, perhaps even just one, but many mares (Levine, 1999; Kavar and Dovic, 2008; Lau *et al.*, 2009; Cieslak *et al.*, 2010; Groeneveld *et al.*,

2010). The practice of using few stallions continues in modern horse breeding due to selection of traits in a limited number of stallions bred to many mares. The fact that one stallion can produce hundreds of offspring a year while a mare can produce only one contributes to the reduction in the number of patrillines. Also, the practicality of keeping mares as opposed to stallions in a herd is an influence on the number of stallions available for breeding. Many modern breeds have been “improved” by the use of relatively few Arabian and Thoroughbred stallions which also could have resulted in the single Y haplotype (Lindgren *et al.*, 2004; Wallner *et al.*, 2004). It should be noted that the use of the term “improved” is used consistently in the historical description of many breeds. It appears to indicate refinement and beautification, even “Arabized” (Clutton-Brock, 1999), although these are subjective nouns that are debatable as to what the desirable traits should be.

In the next section I will continue to expand on this review as it specifically relates the evolution of horses.

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SECTION II: THE DEVELOPMENT OF THE MODERN HORSE

FROM FOUR SUBSPECIES OF *EQUUS CABALLUS*

The diversity of modern horse breeds substantiates the polyphyletic origin of the modern horse. Morphological characteristics along with DNA studies conclude that the domestic horse arose from multiple locations. There is fossil evidence in Eurasia of several types of wild horses, possibly different subspecies, existing in overlapping ranges (Groves, 1974). With the spread of domestication, the ability to use indigenous animals in a breeding program allowed for selection of certain traits. Although this would allow a blending and mixing of DNA, certain groups are distinct. It is my hypothesis that four distinct subspecies identified as “types” by Speed (1952a) followed by Ebhardt (1962) and supported by Skorkowski (1960), had the ability to hybridize and produce fertile offspring that possessed characteristics that appealed to humans for different applications. With continued selection, some of the distinct traits were lost. However, without the diversity of characteristics to begin with, the modern breeds would not have developed to the extent that they have in the relatively short amount of time since domestication.

As domestication events spread across Europe, it is likely that few stallions would have been used on local populations of mares. Clutton-Brock (1999) notes that since by 1500 BC, there was already a difference between northern horse types and desert breed types and finds that it is hard to believe that they did not already originate from several different subspecies. In fact, as early as 1869, M. Sanson described eight subspecies of horses in Northwestern Europe alone (Sanson, 1869). Several authorities have described the diversity of horses indigenous to certain regions (Sanson, 1868; Ewart, 1904; Ridgeway, 1905; Lydekker, 1912; Bennett and Hoffman, 1999; Aberle, 2004). This included James Cossar Ewart who, in 1904, described three species of

primitive horses: 1) *Equus caballus celticus*, or Celtic pony (Fig. 3), 2) *Equus caballus typicus* (which also is found in the literature as *Equus caballus silvaticus* and *Equus caballus germanicus*), the Norse Horse (Fig. 4), and 3) *Equus przewalskii* or Przewalski's horse (Fig. 2).

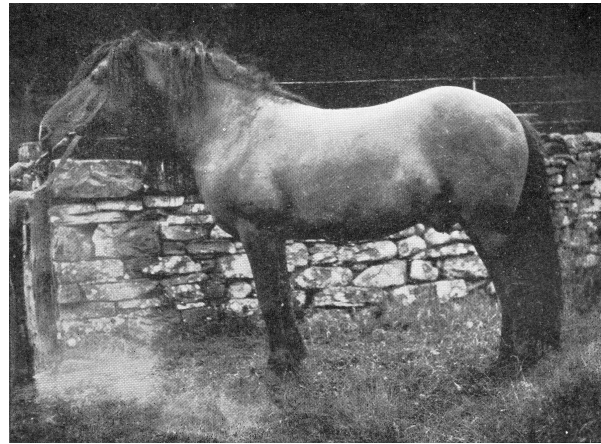
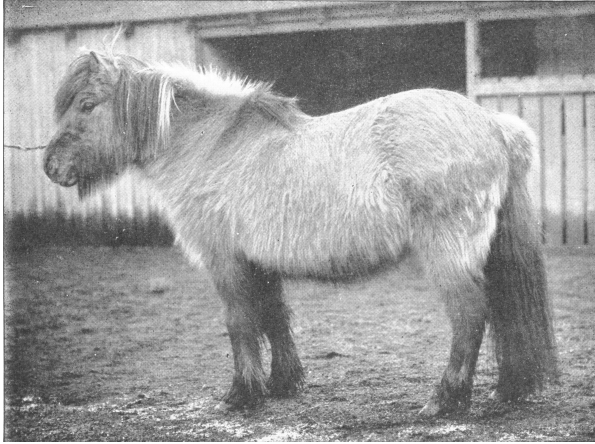


Fig. 3: Celtic Pony: *E. caballus celticus*.

Fig. 4: Norse Horse: *E. caballus typicus*.

Images from *The Multiple Origin of Horses and Ponies* by James Cossar Ewart, 1904.

Fifty years later, Speed and Etherington (1952a) described four primitive types of horses that contributed to the formation of the modern breeds. Research by Ebhardt (1962) further supported this hypothesis and Skorkowski (1960) referred to the Speed/Ebhardt types as

Type 1: *Equus caballus muninensis*

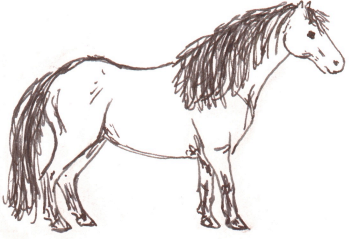
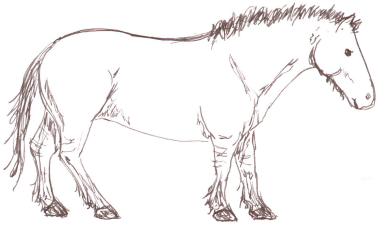
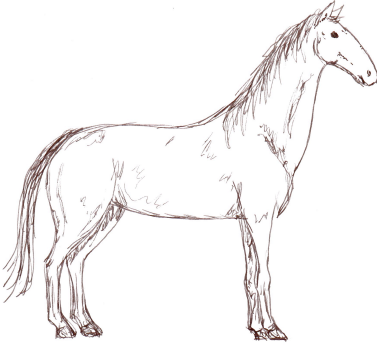
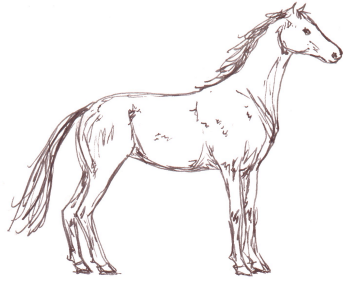
Type 2: *Equus caballus abeli*

Type 3: *Equus caballus mosbachensis*

Type 4: *Equus caballus nordicus*

Modern studies now support this hypothesis with DNA haplotype studies completed by Georgescu et al., (2011). My argument is that it is these four types, which merit the classification as subspecies, are indeed the origin of the modern horse breeds. The types are described in Table 1.

Table 1: Four horse subspecies that contributed to the modern horse

Pony Type 1		standing about 12.2 hands with a stocky body and short legs, croup higher than withers, thick heavy mane and tail, and round hooves
Pony Type 2		standing about 14 hands, heavier build than Type 1, stiff, erect mane, heavy head on low set neck, croup higher than withers, relatively short, thick legs and round hooves
Horse Type 3		tall animal about 16 hands with long body and long legs with oval hooves, withers higher than croup, upright neck and long head with convex profile
Horse Type 4		small animal about 11 hands with horse proportions, withers higher than croup, fine boned legs, oval hooves, small elegant head with concave profile

Drawings by the author.

Other studies have assigned classification of several horse subspecies to areas of domestication (Benett and Hoffman, 1999). According to Benett, the draft horses found in Europe and the ponies of the British Isles have descended from the same subspecies (Benett and Hoffman, 1999). Some early studies in cranial and skeletal morphology also support this hypothesis (Lydekker, 1912). However, recent mtDNA studies lend little support for this hypothesis due to the clustering of the British ponies together as a distinct genetic group (Hovens and Rijkers, 2013; Der Sarkissian *et al.*, 2015). The names assigned by Skorkowski listed above are antiquated and the only one that remains in use is *E.c.mosbachensis*. Bennett and Hoffman (1999) describe four subspecies corresponding to Types 1-4 with the following names, in order: *E.c.caballus*, *E.c.ferus*, *E.c.mosbachensis*, *E.c.pumpelli*.

Once the horse was domesticated, selection for certain traits resulted in different phenotypes or breeds, classified as paraspecies by Groves (1995). Juliet Clutton-Brock (1999) states, “the variation that occurs within the species is described in terms of breeds rather than subspecies.” The difference between the two is that subspecies are found in an isolated region as the result of evolution and breeds are a product of artificial selection where physical geographic barriers do not necessarily play a role. Thus, based on these definitions, the argument could be made that breeds and subspecies are equal; one occurring in nature and one occurring under artificial selection.

In 1915, Orren Lloyd-Jones writes, “A breed is a group of domestic animals termed such by common consent of the breeders.” He then defines a purebred to be, “an animal entered or eligible to entry in the association books, or descended from such animals.” He makes a valid point that the word “purebred” does not hold any definition without the existence of a registry and that “it is in fact a civil, rather than a biological word,” (Lloyd-Jones, 1915). Breeds have

been developed by population bottlenecks, geographical isolation (before advances in modern technology allowed transport and shipping of semen), environmental adaptation due to changes in climate, nutrition, parasites, disease, and by selective breeding by man (Barker, 2001).

Juliet Clutton-Brock (1999) defines “breed” as “a group of animals that has been selected by humans to possess a uniform appearance that is heritable and distinguishes a breed from other groups of animals within the same species.” A more recent definition of “breed” is more detailed: “a separately identified (or identifiable) population or group of interbreeding domestic animals. Identification will usually be based on common physical characters such as color, size, shape, and also on shared genetic and historical origins. A breed is usually associated with a particular ecological zone, geographical area and farming system. Some breeds may, however, be present in multiple countries. Established crosses between two or more breeds may be recognized as a separate breed, but shifting or transitional crossbred groups are not” (Cunningham, 1992).

Analysis of the process of domestication through time shows the Bronze Age (4,000-1,000 B.C.) appears to be the beginning of differentiation of the domestic horse into different types (Clutton-Brock, 1999). By the Iron Age (1000 B.C.), there is evidence of an establishment of at least two distinct types: Pony Type I and Horse Type 3. Archeological equine remains from Britain have skeletal structure proportions similar to the Pony Type 1, whereas those found in Egypt are from long-limbed, tall animals of “horse” proportions similar to Horse Type 3 (Clutton-Brock, 1999). It would be expected that the other two types (Pony Type 2 and Horse Type 4) would be present during the same time period; however no evidence of archeological studies in the geographical regions where these two types would be found could be located.

Table 2: Events and corresponding dates in the development of the modern horse

Year	Era/Age	Events	Epoch
2 Ma BC		<i>Equus caballus</i> occurred throughout North and South America and Eurasia east to Japan; migrations between Alaska occurred	Pleistocene
200,000 BC		genetic divergence of <i>E. caballus</i> into several forms (subspecies)	
50,000 BC	Upper Paleolithic	anatomically modern humans	
10,000 BC		end of last Ice Age; cave paintings in France and Spain; extinction of horses in North and South America; <i>E. caballus</i> survives in Eurasia	Holocene
8,000 BC	Mesolithic	migration of wild horses eastward due to the loss of steppe habitat and an increase of forests in Europe	
5,000 BC	Neolithic	migration of horses from east to west with diffusion of agriculture	
4,000 BC	Bronze Age	multiple domestication events; increase in agricultural societies; horses and chariots appear; extensive trade and diffusion of equitation across Europe and Asia	
1700 BC		chariot use expands throughout Asia and Europe	
1200 BC		cavalry appears	
1000 BC	Iron Age	archeological evidence of Pony Type 1 in Britain and Horse Type 3 in Egypt	
500 BC		steppe nomads in Asia, Scythians in eastern Europe and Celts in western Europe expand cavalry use throughout Eurasia	
0	Roman Empire		
1000 AD	Dark Ages		
1700 AD		Carl Linnaeus introduces taxonomic classification	
1800 AD		Charles Darwin describes evolution	
1900 AD		Ewart and Ridgeway studied and classified subspecies of <i>E. caballus</i> ; Speed, Ebhardt, and Skorkowski supported classification of 4 subspecies described in this paper	

(Matthew, 1926; Simpson, 1961; Goodall, 1977; Forsten, 1989; Gonzaga, 2004)

What is the difference between a “horse” and a “pony?” Since all breeds of horses and ponies are considered *E. caballus*, there should not necessarily be a distinction between “horse” and “pony,” and these terms have no significance in taxonomy (Hovens and Rijkers, 2013). Nevertheless, there are currently two basic morphological definitions for “pony”, one based on height of the animal, and one based on overall conformation type. In regards to height, the definition is any horse that is 14.2 hands and less in height is considered a “pony.” “Pony” conformation is defined as an animal that has relatively short legs in proportion to its body size, stocky bodies, rounded over the withers, profuse mane and tail, shorter heads with broad profiles, and the ability to carry or pull large amounts of weight in relation to overall size. The trot of pony conformation has a shorter stride due to shorter stance and swing durations than that of a horse (Back *et al.*, 1999). “Horse” conformation is described as having long limbs in relation to body size with less profuse mane and tail, and a slick, short coat. Horse conformation has more extension of the elbow, stifle, and tarsal joints and more flexion of the hip joint during the midstance of the trot than does pony conformation (Back *et al.*, 1999).

Although there are over 1400 modern horse breeds listed in the Domestic Animal Diversity System database, we can still find modern day examples of the original four types. These examples would include: Pony Type 1 represented by the Exmoor pony; Pony Type 2 represented by the Norwegian Fjord Horse and Icelandic Horse; Horse Type 3 represented by the Akhal-Teké; and Horse Type 4 represented by the Caspian Horse.

Pony Type 1

A living example of this type is the Exmoor Pony (Fig. 5), a robust animal standing about 12 hands high that continues to roam the moorlands of Exmoor, England (Speed and Etherington, 1952a; 1952b; 1953; Speed, 1956) . They exhibit classic “pony” conformation typical of Type I subspecies: stocky bodies with relatively short legs, profuse mane and tail, rounded withers, and short heads with broad profiles. Evidence of subspecies status exists in the fact that there is complete uniformity in the morphology of these ponies. Prezwalski’s horses are the only other horses that exhibit uniformity of coat color (Hovens and Rijkers, 2013). The Exmoor ponies currently live in the wild, subsisting on meager rations found in their natural environment. Their skeletal features are identical to those found in the frozen tundra horse of the extinct species *E. caballus alaskae* (Speed and Etherington, 1952a; Baker, 2008). Recent mtDNA studies have concluded that the Exmoor pony is a wild type horse that has not been influenced by domestic breeds (Hovens and Rijkers, 2013).



Fig. 5: Mary Speed with an Exmoor Pony.
Photo from *Exmoor Ponies: Survival of the Fittest* by Sue Baker, 2008.

Pony Type 2

Pony Type 2 is generally described as a large “pony” breed, proportionally, yet it is the size of a small horse and is quite powerful and usually used for draft work. Two examples are the Norwegian Fjord and Icelandic.

The Norwegian Fjord horse (Fig. 6) has a primitive appearance, similar to that of the Przewalski horse with pony proportions in a small draft horse size. All Fjords are dun with a dorsal stripe and zebra striping on the legs, some individuals possessing more markings than others. The dun gene is always present but may be on a base of bay, chestnut, or black, therefore giving rise to a variety of dun coloration in the breed. Fjord horses have stiff mane that, when trimmed, remains erect like that of the Przewalski. Their skin is very thick and somewhat loose, different from other horses, and the hairs are coarser than other horse breeds. Excavation of Viking burial sites shows evidence of the Fjord horse from 2000 years ago (Norwegian Fjord Horse Registry). Although the uniformity of the breed is definitive, strict selection for consistent type did not begin until the 19th century before which other coat colors and patterns existed in the breed.



Fig. 6: Norwegian Fjord with natural mane.
Photo by the author.

The Icelandic horse (Fig. 7) also fits into Pony Type 2 classification due to its conformation and size. They are extremely hardy animals that possess great strength in proportion to their overall size. It is also unique in that it has the ability for an ambling gait referred to as the tölt. The Icelandic horse has been isolated on an island for over 1,000 years and is believed to have descended from a species referred to in the literature as *E. scandinavicus* (Hugason, 1994). It is believed that this species, most likely actually a subspecies, crossbred with other subspecies of *E. caballus* to form other northern breeds except in Iceland where the horses remained isolated after the importation of ponies of the Western Isles of Scotland in 870 A.D (Speed and Etherington, 1952b). Morphological and genetic studies revealed that the Icelandic horse is closely related to the Shetland pony (Speed and Etherington, 1952b; Hugason, 1994) and to the Norwegian Fjord which all show a close relation to the Mongolian horse (Fig. 8) (Bjørnstad *et al.*, 2003; Der Sarkissian *et al.*, 2015). Interestingly, the Mongolian horse also has the ability to tölt, is of similar size and stature to the Icelandic horse and is found in the same coat colors and patterns. Given the isolation of the Icelandic horse after domestication and the spread of the Mongolian nomads into Europe, the Icelandic horse appears to be a living relic of the type of horses that were imported to Iceland over 1,000 years ago.



Fig. 7: Pony Type 2: Icelandic horses.
Photo by the author.

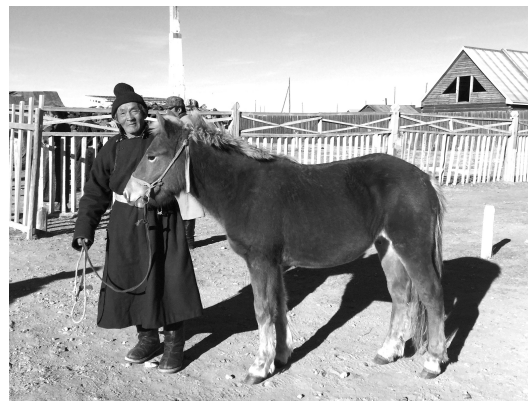


Fig. 8: Pony Type 2: Mongolian horse.
Photo by Dr. Kydee Sheetz.

Horse Type 3

The Akhal-Teké (Fig. 9) is a modern day example of the description of Horse Type 3 with characteristic “horse” conformation: long legs in relation to depth of chest and a long back. It is a fairly tall animal with an upright neck and a long head. Developed in the desert, the coat is very fine and satin like often with a metallic sheen. DNA studies group the Akhal-Teké with the other desert breeds (Cothran, 1994; Georgescu *et al.*, 2011; Warmuth *et al.*, 2011).

The Akhal-Teké is considered an ancient breed that was used as a war horse by nomadic tribes, taking their name from the Teké tribe (Keyser-Tracqui *et al.*, 2005). Hendricks (1995) states that the Akhal-Teké is the purest descendent of the ancient Scythian horse as the Exmoor Pony is to the Celtic pony. The Scythian horse and the Celtic pony have been identified as a way to describe the horses used in early domestication (Gonzaga, 2004). The Scythians were a nomadic tribe from Asia and the Celts were tribes that invaded Western Europe during the cavalry revolution of 600-500 B.C. (Gonzaga, 2004; see Table 2).



Fig. 9: Horse Type 3: Akhal-Teké horse.
Photo by the author.

Horse Type 4

The Caspian Horse (Fig. 10), a relatively small horse from the north of Iran, is the ideal representative of the original Horse Type 4. These horses were only recently rediscovered and brought to the equine world's attention in 1965 by Louise Firouz, at which time they were believed to be living specimens of *E. fossilis persicus*, the extinct Persian fossil horse (Firouz, 1971, 1998). Previously, in 1904, Dr. J. U. Duerst had described the Persian fossil horse as the direct ancestor of the Arabian, naming them *E. caballus pumelli* (Duerst, 1908, Lydekker, 1912). At the time of his description, the Arabian was a familiar breed and the Caspian had not yet been rediscovered.

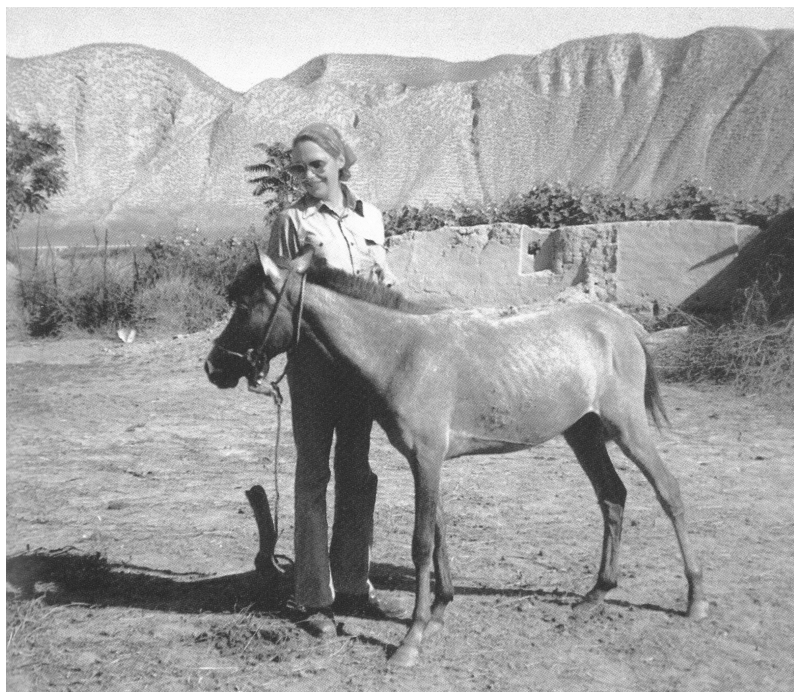


Fig. 10: Horse Type 4: Caspian Horse. Mature horse with Louise Firouz in Iran. Photo from *Allen Guide to Horse and Pony Breeds: The Caspian Horse* by Brenda Dalton, 2000.

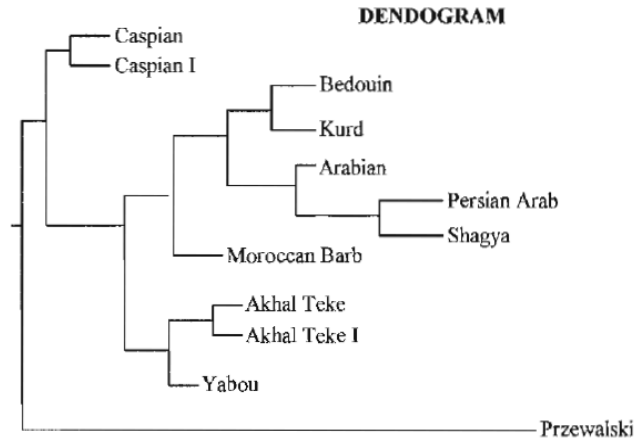


Fig. 11: Dendrogram showing relationships between the Caspian and other desert breeds. Image from *The Original Ancestors of the Turkoman, Caspian Horses* by L. Firouz, 1998.

Current genetic research of mtDNA places the Caspian in a sister group to the Akhal-Teké and the Arabian (Cothran, 1994; see Fig. 11). Previously, the Arabian was considered the primary example of Horse type 4 until the description of the Caspian. The figure indicates that the Caspian and all the other Oriental (desert) breeds share a common ancestor. As the Caspian appears on the top, the lower branch breaks into the types of Arabians and the Akhal-Tekés (the Yabou is the same breed, just not bred by the Teké tribe). The distant relative, the Przewalski horse is shown as an outlier.

The Caspian horses resemble small horses found on the artifacts of King Darius of Persia that were previously believed to be extinct (Firouz, 1978; Amirinia *et al.*, 2007). The Caspian is unique in that an individual may have either 64 or 65 chromosomes naturally occurring within a breeding population (Hatami-Monazah and Pandit, 1979). In 1972, Shahresevi and Hosseinion in Preliminary Report on the Basic Skeletal Differences of the Caspian Miniature Horse as

Compared to Other Iranian and European Breeds described the following morphological characteristics:

1. absence of a parietal crest in the skull (see Fig. 12)
2. length of the spinous processes of the first six thoracic vertebrae are longer in relation to the size of the vertebrae than other horses
3. the scapula is the shape of an isosceles triangle and resembles that of a ruminant
4. the metapodials are longer and slimmer relative to the size of the horse compared to other breeds

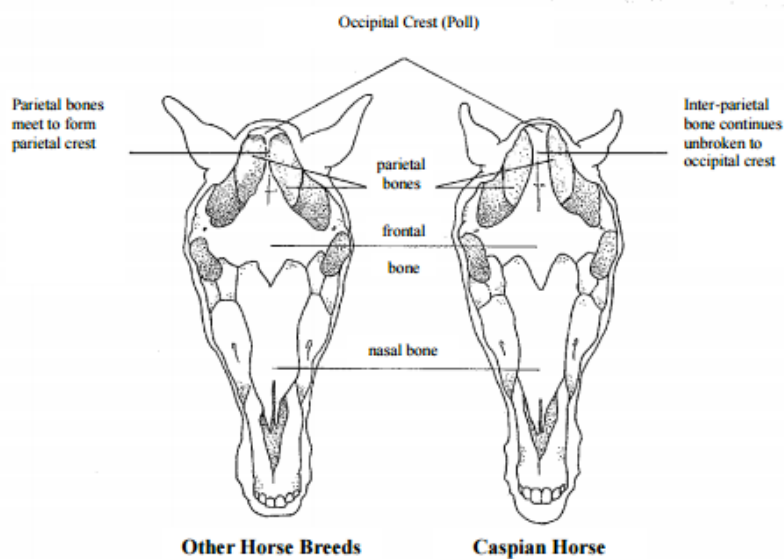


Fig. 12: Comparison of Caspian skull with skull of other horse breeds. Drawing by Lez Harvey from *The Caspian Horse* by Brenda Dalton, 1999.

Due to its unique karyotype being identical to that of the hybrid between *E. przewalski* and *E. caballus*, it has been hypothesized that the Caspian is a hybrid between these two species (Hatami-Monazah and Pandit, 1979). Is it possible that the Caspian horse is frozen in time

between a $2n=66$ animal, such as *E. przewalski* and what was to become the domesticated horse of $2n=64$? It appears that the Caspian is unique in that it was tamable and easily domesticated.

Conclusion

The four subspecies described in this paper represent the ancestral types that gave rise to our modern breeds. These subspecies were indigenous to both the desert regions and northern Europe and Asia and had evolved through natural selection in response to their environment. Once the domestication process began, these individual subspecies were selectively bred through artificial selection to meet the needs of the humans in those particular regions of the world. Although we now have the blending of many breeds together, examples of the original types can still be identified.

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