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A REINTRODUCED NATIVE WILDLIFE SPECIES**

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**THE NORTH AMERICAN WILD HORSE:  
A REINTRODUCED NATIVE WILDLIFE SPECIES**

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**ABSTRACT**

*The wild horse of North America is classified as a non-native species by many government agencies. The basis for this classification is the assumption that the horse species that disappeared from North America 7,600 years ago was not the same species returned to the continent in 1519 and thereafter. Neither paleontological nor molecular biology data support this classification as a different species. "Over-splitting" of early caballine horse species was based largely on phenotypic differences and is subjective in nature. Modern molecular biology techniques, including mitochondrial and ancient DNA analysis support the existence of *Equus caballus* in North America long before its disappearance during megafaunal extinction. While domestication of *E. caballus* is often cited as reason to classify the horse as non-native, this behavioral plasticity did not create a new species. Sound science and biology confirm today's North American horse as the same species that originated and inhabited North America prior to its disappearance. Thus, this species must be classified as a reintroduced native species.*

## INTRODUCTION

Are North American wild horses truly "wild," representing an indigenous species, or are they so far removed genetically from their prehistoric origins and ancestors that they may be considered "exotic" and "non-native?" The question at hand is, therefore, whether or not modern horses, *Equus caballus*, as they exist wild today in North America, should be considered native wildlife.

The question is legitimate. In North America, the wild horse is often labeled as a non-native or exotic species by most federal or state agencies charged with the responsibility for wildlife management on public lands, such as the National Park Service, U.S. Fish and Wildlife Service, and the Bureau of Land Management. The legal mandate for many of these agencies is to protect native wildlife and prevent non-native species from causing harmful effects on the general ecology of the land. A great deal of the current management policy for wild horses is dictated by federal law; however, it is also influenced by the designation of the horse as native or non-native. Thus, the rationale for examining whether the North American horse is a native or non-native species is significant from a legal standpoint, but equally interesting from a purely biological viewpoint.

Critics of the idea that the North American wild horse is a native animal, using only selected palaeontological data, assert that the species, *E. caballus*, which was reintroduced to North America in 1519, was a different species from that which disappeared, during megafaunal extinction, between 13,000-7,600 years before. Herein lies the crux of the

debate. However, neither paleontological opinion nor modern molecular genetics support the contention that the wild horse in North America is non-native.

The genus *Equus*, which includes modern horses, zebras, and asses, is the only surviving genus in a once diverse family (Equidae) that included 27 genera. The precise date of origin for the genus *Equus* is unknown, but evidence documents the dispersal of *Equus* from North America to Eurasia approximately 2-3 million years ago and a possible origin at about 3-5 million years ago. Following this original emigration, several extinctions occurred in North America, with additional migrations to Asia (presumably across the Bering Land Bridge), and return migrations back to North America, over time. The last North American disappearance probably occurred between 13,000 and 11,000 years ago (McFadden 2005) although more recent disappearances for horses have been suggested. Ross MacPhee, Curator of Mammalogy, American Museum of Natural History, and colleagues, have dated the existence of woolly mammoths and horses in North America as recently as 7,600 years ago (Halle et al. 2009). Had it not been for previous westward migration, over the Bering Land Bridge, into northwestern Russia (Siberia) and Asia, the horse would have faced complete world-wide extinction. However, *Equus* survived and spread to all continents of the globe, except Australia and Antarctica.

In 1493, on Columbus' second voyage to the Americas, Spanish horses, representing *E. caballus*, were brought back to North America, first in the Virgin Islands, and, in 1519, they were reintroduced on the continent, in modern-day Mexico, from where they radiated throughout the American Great Basin and Great Plains, after escape from their owners or by pillfering (Fazio 1995).

## FOSSIL EVIDENCE

*Equus*, a monophyletic taxon, is first represented in the North American fossil record about four million years ago by *E. simplicidens*, and this species is directly ancestral to later Blancan species about three million years ago (Azzaroli and Voorhies 1990). Azzaroli (1992) believed, again on the basis of fossil records, that *E. simplicidens* gave rise to the late Pliocene *E. Idahoensis*, and that species, in turn, gave rise to the first caballine horses approximately two million years ago in North America (Eisenmann 1992; Forstén 1992). This taxonomic division within that timeline, between caballines and non-caballines on the basis of morphological data, has been supported by Forstén (1992) and validated on a molecular genetics basis as well (Lowenstein and Ryder, 1985; George and Ryder 1986; Oakenfull and Clegg, 1998; Kruger et al, 2005). Some caballines migrated to Asia about one million years ago, while others, such as *E. c. niobrarensis*, remained in North America.

In North America, diversification of the caballines into separate species and breeds has been estimated to occur about 250,000 years ago (Steiner and Ryder 2011), and included *E. caballus*, *E. caballus mexicanus*, or the American Periglacial Horse (also known as *E. caballus laurentius* Hay, or *midlandensis* Quinn) among others (Hibbard 1955). Today, we would recognize these latter two horses as breeds of *E. caballus*. In North America, isolated lower molar teeth and a mandible from sites of the Irvingtonian age appear to be *E. caballus*, morphologically. Through most of the Pleistocene Epoch in North America, the commonest species of *Equus* were not caballines but other lineages (species) resembling zebras, hemiones, and possibly asses (McGrew 1944; Quinn, 1957). The divergence of caballines into *E. przewalskii* and *E. caballus* about 250,000 years ago is

near the ranges derived from studies of horse evolution using mtDNA (Oakenfull et al. 2000), nuclear genetics (Wallner et al. 2003), and microsatellite studies (Kruger et al. 2005). Even more recent data makes clear that *E. przewalskii* was not the progenitor of *E. caballus*, and that the two species diverged from a common ancestor between 123,000 and 241,000 years ago (Goto et al. 2011). Collectively, these studies make clear, in an incontrovertible fashion, the divergence of *E. caballus* well before its disappearance from North America.

Thus, based on a great deal of paleontological data, the origin of *E. caballus* is thought to have diverged about 250,000 years ago, and it originated in North America. However, the determination of species divergence based on phenotype is at least modestly subjective and often fails to account for the differing phenotypes within a species, described above. Purely taxonomic methodologies looked at physical form for classifying animals and plants, relying on visual observations of physical characteristics. While earlier taxonomists tried to deal with the subjectivity of choosing characters they felt would adequately describe, and thus group, genera and species, these observations were lacking in precision. Nevertheless, the more subjective paleontological data strongly suggests the origin of *E. caballus* somewhere between 125,000 and 250,000 years ago.

#### THE MOLECULAR BIOLOGY DATA

Reclassifications are now taking place, based on the power and objectivity of molecular biology. If one considers primate evolution, for example, molecular biology has produced a new and different evolutionary pathway for humans, and this science has described entirely different relationships with other primates. None of this would have been

possible prior to the methodologies now available through mitochondrial-DNA (mtDNA) analysis, and more recently, ancient DNA analysis (aDNA). How do the molecular genetics data compare with the paleontological data?

According to the work of researchers from Uppsala University of the Department of Evolutionary Biology (Forstén 1992), the date of origin, based on mutation rates for mtDNA, for caballine horses, is set at approximately 1.7 million years ago in North America. This, of course, is very close, geologically speaking, to the 1-2 million-year figure presented by the interpretation of the fossil record. In another study, Kruger et al. (2005), using microsatellite data, confirms the work of Forstén (1992) but gives a wider range for the emergence of the caballine horse, of 0.86 to 2.3 million years ago. At the latest, however, that still places the caballine horse in North America 860,000 years ago. Thus, the proposed divergence of caballines based on morphological data is supported by molecular data as well. The issue now shifts to the divergence of *E. caballus*.

Initially rare in North America, caballine horses were associated with stenoid horses (perhaps ancestral forerunners but certainly distinct species), but between one million and 500,000 years ago, the caballine horses replaced the stenoid horses probably because of climatic preferences and changes in ecological niches (Forstén 1988). By the late Pleistocene, the North American taxa that can definitely be assigned to *E. caballus* are *E. caballus alaskae* (Azzaroli 1995) and *E. caballus mexicanus* (Winans 1989 – using the name *laurentius*). Both ecomorphotypes of *E. caballus* were thought to have been derived from *E. c. niobrarensis* (Azzaroli 1995). By ecomorphotype, we refer to differing phenotypic or physical characteristics within the same species, caused by genetic isolation in discrete habitats.

A series of genetic analyses, carried out at the San Diego Zoological Society's Center for Reproduction in Endangered Species, and based on chromosome differences (Benirschke et al. 1965) and mtDNA (George and Ryder 1986) both indicate significant genetic divergence among several forms of wild *E. caballus* as early as 200,000-300,000 years ago. Thus, the origin of *E. caballus* had to be earlier, but, at the very least, well before the disappearance of the horse in North America between 13,000-7,600 years ago.

Mitochondrial DNA analysis, has recently revealed that the modern horse, *E. caballus*, is genetically equivalent to *E. lambei* (the Yukon horse), a horse, according to fossil records, that represented the most recent *Equus* species in North America prior to disappearance. Not only is *E. caballus* genetically equivalent to *E. lambei*, but no fossil evidence exists for the origin of *E. caballus* anywhere except North America (Forstén 1992). Carlos Vilà, also of the Department of Evolutionary Biology at Uppsala University, has corroborated Forstén's work. Vilà et al. (2001) have shown that the origin of domestic horse lineages was extremely widespread, over time and geography, and supports the existence of *E. caballus* in North America before its disappearance, corroborating the work of Benirschke et al. (1965), George and Ryder (1995), and Hibbard (1955).

A study conducted at the Ancient Biomolecules Centre of Oxford University (Weinstock et al. 2005) also corroborates the conclusions of Forstén (1992). Despite a great deal of variability in the size of the Pleistocene equids from differing locations (mostly ecomorphotypes), the DNA evidence strongly suggests that all of the large and small caballine samples belonged to the same species. The study concluded that "The presence of a morphologically variable caballine species widely distributed both north



and south of the North American ice sheets raises the tantalizing possibility that, in spite of many taxa named on morphological grounds, most or even all North American caballines were members of the same species." The work of Hofreiter et al. (2001), examining the genetics of the so-called *E. lambei* from the permafrost of Alaska, found that the variation was within that of modern horses, which translates into *E. lambei* being genetically indistinguishable from *E. caballus*. The molecular biology evidence is incontrovertible, but it is also supported by the interpretation of the fossil record, as well.

Following Hofreiter's elegant work, a team of British and German investigators sought the answer to the question of whether today's horse, *E. caballus*, is the descendent of one or more post-glacial primitive horses. Using mtDNA D-loop sequencing they examined the relatedness between 318 horses from 25 Oriental and European breeds, North American wild horses, and Mongolian wild horses, as well as published data from prehistoric permafrost horses (amounting to a total of 652 horses). The results showed the presence of 93 different mtDNA types, which grouped into 17 distinct phylogenetic clusters, or genotypes. Within the domestic horse populations, including North American wild horses, the number of different mtDNA types indicates the presence of different post-glacial horses in the founding population. Further, six of the eight samples of aDNA from Alaskan permafrost horses clustered monophyletically, representing a single genotype (Jansen et al. 2002). This work confirmed the conclusions of Vilà et al. (2001) cited above.

Two more recent studies found evidence for taxonomic "oversplitting" from species to generic levels. Orlando et al. (2008), using ancient DNA analysis and a rigorous

phylogenetic approach, found that *Equus (Amerhippus)* was merely a variant (breed) of *E. caballus*. Following that, Orlando et al. (2009) examined the evolutionary history of a variety of non-caballine equids across four continents, found additional evidence for taxonomic “oversplitting” from species to generic levels. This oversplitting was based primarily on late-Pleistocene fossil remains without the benefit of molecular data. A co-author of this study, Dr. Alan Cooper, of the Australian Centre for Ancient DNA, concluded, “Overall, the new genetic results suggest that we have underestimated how much a single species can vary over time and space, and mistakenly assumed more diversity among extinct species of megafauna.”

Still another approach to understanding the origins of equine species has taken the form of revealing the complete genome sequence of the domestic horse. This approach, conducted by 59 collaborative scientists at 33 different institutions, also shed light on the origins of *E. caballus* (Wade et al. 2009), and the results suggest an even earlier origin of the modern horse, at about 3 mya, at such time as the genus *Equus* split into 8 or 9 different species, including *E. caballus*. Work of this nature even confirms the similar social organization of those early horses, and reveals that *E. caballus* originated from very few males and many females, a pattern consistent with the species’ social organization today (Lau et al. 2009).

## DOMESTICATION

The fact that horses were domesticated before they were reintroduced matters little from a biological viewpoint, if we view either genetics, as we have seen above, or social organization and behavior as an evolutionary endpoint. Some opposition to the

contention that North America's wild horses are a native species centers around unpublished claims that possible – and probable – changes in nuclear gene frequencies as a result of intensive selection during domestication. While it is probable that the speculative nuclear gene frequencies have changed over time, horses remain the same genus and species (*Equus caballus*) that originated in North America, and whether or not they were domesticated or nuclear gene frequency has changed is quite irrelevant. Selective breeding is simply a human-induced form of genetic isolation, which, as has been noted earlier, causes various ecomorphotypes within a species in the wild. Domestication altered nothing in the way of social organization or behavior, and we can see that in the phenomenon called “going wild,” where wild horses revert to ancient behavioral patterns. Feist and McCullough (1976) dubbed this “social conservation” in their paper on behavior patterns and communication in the Pryor Mountain wild horses of Montana/Wyoming. The reemergence of primitive behaviors, resembling those of the plains zebra, indicated to the authors the shallowness of domestication in horses.

The modern horse also appears to have retained ancient physiological traits as well, despite domestication and whatever changes in nuclear gene frequency may have occurred. It is a common trait of northern latitude ungulates, such as roe deer (Weiner 1977) and red deer (Arnold et al. 2004) to be capable of hypometabolism in cold weather and food scarcity, as a survival mechanism. The Przewalski horse has also been shown to be able to adjust metabolism downward diurnally and seasonally in the winter (Arnold et al. 2006; Kuntz et al. 2006). Recently, it has also been demonstrated that Shetland ponies are capable of the same hypometabolic adjustments (Brinkmann et al. 2012), maintaining

ancient physiological adjustments despite domestication. This reinforces the concept of the limited genetic change as a result of domestication.

Still another often used argument against the native status for wild horses, is that they were domesticated successfully, while the Przewalski's horse (*E. przewalskii* - the Mongolian wild horse) was never domesticated, and therefore the latter is the only truly wild horse. This argument deals less with the point of origin or genetics for the North American horse than it does for the arbitrary designation as "wild." Yet this same argument ignores the fact that the pre-domesticated wild horse was merely sufficiently behaviorally pliable to be domesticated in the first place.

The issue of feralization and the use of the word "feral" is a human construct that has little biological meaning except in transitory behavior, forced on the animal in some manner. Consider this parallel. Przewalski's horse disappeared from Mongolia a hundred years ago, although some unverified reports suggested some animals were still present in the 1960s. It has survived since then in zoos. That is not domestication in the classic sense, but it is captivity, with keepers providing food and veterinarians providing health care. Then they were released during the 1990s and now repopulate their native range in Mongolia. Are they a reintroduced native species or not? Thus, there is little difference between them and *E. caballus* in North America, except for the time frame and degree of captivity. It is also probable that the intensive captive breeding, even over a hundred years, has changed the nuclear gene frequency in *E. przewalskii*, particularly because of the small founder population.

The key elements in describing an animal as a native species are (1) where it originated, and (2) whether or not it co-evolved with its habitat. Clearly, *E. caballus* did both, here in North America. There might be arguments about “breeds,” but there are no scientific grounds for arguments about species. The issue of co-evolving with the habitat is also a weak argument. Consider that the North American horse diverged about 250,000 years ago and co-evolved with the vegetation until very recently, geologically speaking. Although there have been redistributions of vegetation since the disappearance of *E. caballus* 7,600 years ago, the plants themselves remain. Some have suggested that the vegetation co-existing with *E. caballus* before its disappearance have lost their adaptations to grazing pressures, which resulted from more than a million years of co-evolution with equids (Lodge 1962). But no evidence for this assertion exists. Thus, the non-native, feral, and exotic designations given by agencies, mandated by law to use “best available science” in decision-making, are not a reflection of sound available science.

Native status for wild horses might place these animals, under law, within a new category for management considerations, although it is uncertain that current federal law designating both protection and management obligations will change. As a form of wildlife, possessing the ancestral genetics of their North American progenitors, the translation of this genetic information into ancient behavioral patterns, and the morphology and biology of a sensitive prey species, the wild horse in North America might more accurately be classified as a reintroduced native wildlife species.

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