

Are wild horses truly "wild," as an indigenous species in North America, or are they "feral weeds" - barnyard escapees, far removed genetically from their prehistoric ancestors? The question at hand is, therefore, whether or not modern horses, *Equus caballus*, should be considered native wildlife.

The question is legitimate, and the answer important. In North America, the wild horse is often labeled as a non-native, or even an exotic species, by most federal or state agencies dealing with wildlife management, 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. Thus, management is often directed at total eradication, or at least minimal numbers. If the idea that wild horses were, indeed, native wildlife, a great many current management approaches might be compromised. Thus, the rationale for examining this proposition, that the horse is a native or non-native species, is significant.

The genus *Equus*, which includes modern horses, zebras, and asses, is the only surviving genus in a once diverse family of horses 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 3.4-3.9 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 extinction probably occurred between 13,000 and 11,000 years ago (Fazio 1995), although more recent extinctions for horses have been suggested. Dr. Ross MacPhee, Curator of Mammalogy at the American Museum of Natural History, and colleagues, have dated the existence of woolly mammoths and horses in North America to as recent as 7,600 years ago. 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 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 Plains, after escape from their owners or by pilfering (Fazio 1995).

Critics of the idea that the North American wild horse is a native animal, using only selected paleontological data, assert that the species, *E. caballus* (or the caballoid horse), which was introduced in 1519, was a different species from that which disappeared between 13,000-11,000 years before. Herein lies the crux of the debate. However, neither paleontological opinion nor modern molecular genetics support the contention that the modern horse in North America is non-native.

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 caballoid horses two million years ago in North America. Some migrated to Asia about one million years ago, while others, such as *E. niobrarensis*, remained in North America.

In North America, the divergence of *E. caballus* into various ecomorphotypes (breeds) included *E. caballus mexicanus*, or the American Periglacial Horse (also known as *E. caballus laurentius* Hay, or *E. midlandensis* Quinn) (Hibbard 1955). Today, we would recognize these latter two horses as breeds, but in the realm of wildlife, the term used is subspecies. By ecomorphotype, we refer to differing phenotypic or physical characteristics within the same species, caused by genetic isolation in discrete habitats. 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). Initially rare in North America, caballoid horses were associated with stenoid horses (perhaps ancestral forerunners but certainly distinct species), but between one million and 500,000 years ago, the caballoid horses replaced the stenoid horses 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 subspecies were thought to have been derived from *E. niobrarensis* (Azzaroli 1995).

Thus, based on a great deal of paleontological data, the origin of *E. caballus* is thought to be about two million 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 ecomorphotypes 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 one and two million years ago.

Reclassifications are now taking place, based on the power and objectivity of molecular biology. If one considers primate evolution, for example, the molecular biologists have provided us with a completely different evolutionary pathway for humans, and they have described entirely different relationships with other primates. None of this would have been possible prior to the methodologies now available through mitochondrial-DNA analysis.

A series of genetic analyses, carried out at the San Diego Zoo's Center for Reproduction in Endangered Species, and based on chromosome differences (Benirschke et al. 1965) and mitochondrial genes (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. These studies do not speak to the origins of *E. caballus* per se, but they do point to a great deal of genetic divergence among members of *E. caballus* by 200,000 to 300,000 years ago. Thus, the origin had to be earlier, but, at the very least, well before the disappearance of the horse in North America between 13,000-11,000 years ago. The relatively new (30-year-old) field of molecular biology, using mitochondrial-DNA analysis, has recently revealed that the modern or caballine horse, *E. caballus*, is genetically equivalent to *E. lambei*, a horse, according to fossil records, that represented the most recent *Equus* species in North America prior to extinction. Not only is *E. caballus* genetically equivalent to *E. lambei*, but no evidence exists for the origin of *E. caballus* anywhere except North America (Forstén 1992).

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 mitochondrial-DNA, for *E. caballus*, 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.

Carles 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 the caballoid horse in North American 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 author states, "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."

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 caballoid horse, of 0.86 to 2.3 million years ago. At the latest, however, that still places the caballoid horse in North America 860,000 years ago. 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* actually being *E. caballus*, genetically. The molecular biology evidence is incontrovertible and indisputable, but it is also supported by the interpretation of the fossil record, as well.

Finally, very recent work (Orlando et al. 2009) that examined the evolutionary history of a variety of non-caballine equids across four continents, found 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, stated, "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."

The fact that horses were domesticated before they were reintroduced matters little from a biological viewpoint. They are the same species that originated here, and whether or not they were domesticated is quite irrelevant. Domestication altered little biology, 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 his paper on behavior patterns and communication in the Pryor Mountain wild horses. The reemergence of primitive behaviors, resembling those of the plains zebra, indicated to him the shallowness of domestication in horses.

The issue of feralization and the use of the word "feral" is a human construct that has little biological meaning except in transitory behavior, usually forced on the animal in some manner. Consider this parallel. *E. Przewalski* (Mongolian wild horse) disappeared from Mongolia a hundred years ago. 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? And what is the difference between them and *E. caballus* in North America, except for the time frame and degree of captivity?

The key element in describing an animal as a native species is (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 non-native, feral, and exotic designations given by agencies are not merely reflections of their failure to understand modern science but also a reflection of their desire to preserve old ways of thinking to keep alive the conflict between a species (wild horses), with no economic value anymore (by law), and the economic value of commercial livestock.

Native status for wild horses would place these animals, under law, within a new category for management considerations. As a form of wildlife, embedded with wildness, ancient behavioral patterns, and the morphology and biology of a sensitive prey species, they may finally be released from the "livestock-gone-loose" appellation.

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Literature cited

- Azzaroli, A. 1990. The genus *Equus* in Europe. pp. 339-356 in: *European Neogene mammal chronology* (E.H. Lindsay, V. Fahlbuech, and P. Mein, eds.). Plenum Press, New York.
- Azzaroli, A. 1992. Ascent and decline of monodactyl equids: A case for prehistoric overkill. *Annales Zoologica Fennici* 28:151-163.
- Azzaroli, A. 1995. A synopsis of the Quaternary species of *Equus* in North America. *Bollettino della Societa Paleontologica Italiana*. 34:205-221.
- Azzaroli, A., and M.R. Voorhies. 1990. The genus *Equus* in North America: The Blancan species. *Paleontologica Italiana* 80:175-198.
- Benirschke K., N. Malouf, R.J. Low, and H. Heck. 1965. Chromosome compliment: Difference between *Equus caballus* and *Equus przewalskii* Polliakoff. *Science* 148:382-383.

- Fazio, P.M. 1995. "The Fight to Save a Memory: Creation of the Pryor Mountain Wild Horse Range (1968) and Evolving Federal Wild Horse Protection through 7 1971," doctoral dissertation, Texas A&M University, College Station, p. 21.
- Feist, J.D., and D.R. McCullough, Behavior Patterns and Communication in Feral Horses, *Z. Tierpsychol.* 41:337-371.
- Forstén, A. 1988. Middle Pleistocene replacement of stenoid horses by caballoid horses ecological implications. *Paleogeography, Paleoclimatology, Paleoecology* 65:23-33.
- Forstén, A. 1992. Mitochondrial-DNA timetable and the evolution of Equus: Comparison of molecular and paleontological evidence. *Ann. Zool. Fennici* 28: 301-309.
- George, Jr., M., and O.A. Ryder. 1986. Mitochondrial DNA evolution in the genus Equus. *Mol. Biol. Evol.* 3:535-546.
- Hibbard C.W. 1955. Pleistocene vertebrates from the upper Becarra (Becarra Superior) Formation, Valley of Tequixquiac, Mexico, with notes on other Pleistocene forms. *Contributions from the Museum of Paleontology, University of Michigan*, 12:47-96.
- Hofreiter, M., Serre, D. Poinar, H.N. Kuch, M., Pääbo, S. 2001. Ancient DNA. *Nature Reviews Genetics*. 2(5), 353-359.
- Kruger et al. 2005. Phylogenetic analysis and species allocation of individual equids using microsatellite data. *J. Anim. Breed. Genet.* 122 (Suppl. 1):78-86.
- McGrew, P.O. 1944. An early Pleistocene (Blancan) fauna from Nebraska. *Field Museum of Natural History, Geology Series*, 9:33-66.
- Orlando, L. et al. 2009. Revising the recent evolutionary history of equids using ancient DNA. *Proc. Nat. Acad. Sci.* www.pnas.org/doi/10.1073/pnas.0903672106
- Quinn, J.H. 1957. Pleistocene Equidae of Texas. University of Texas, Bureau of Economic Geology, Report of Investigations 33:1-51.
- Vilà, C., J.A. Leonard, A. Götherström, S. Marklund, K. Sandberg, K. Lidén, R. K. Wayne, H. Ellegren. 2001. Widespread origins of domestic horse lineages. *Science* 291: 474-477. 8
- Weinstock, J.E., A. Sher Willerslev, W. Tong, S.Y.W. Ho, D. Rubenstein, J. Storer, J. Burns, L. Martin, C. Bravi, A. Prieto, D. Froese, E. Scott, L. Xulong, A. Cooper. 2005. Evolution, systematics, and the phylogeography of Pleistocene horses in the New World: a molecular perspective. *PLoS Biology* 3:1-7.

Winans M.C. 1989. A quantitative study of North American fossil species of the genus *Equus*. pp. 262-297, in: *The Evolution of Perissodactyles* (D.R. Prothero and R.M. Schoch, eds.). Oxford University Press, New York, NY.

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