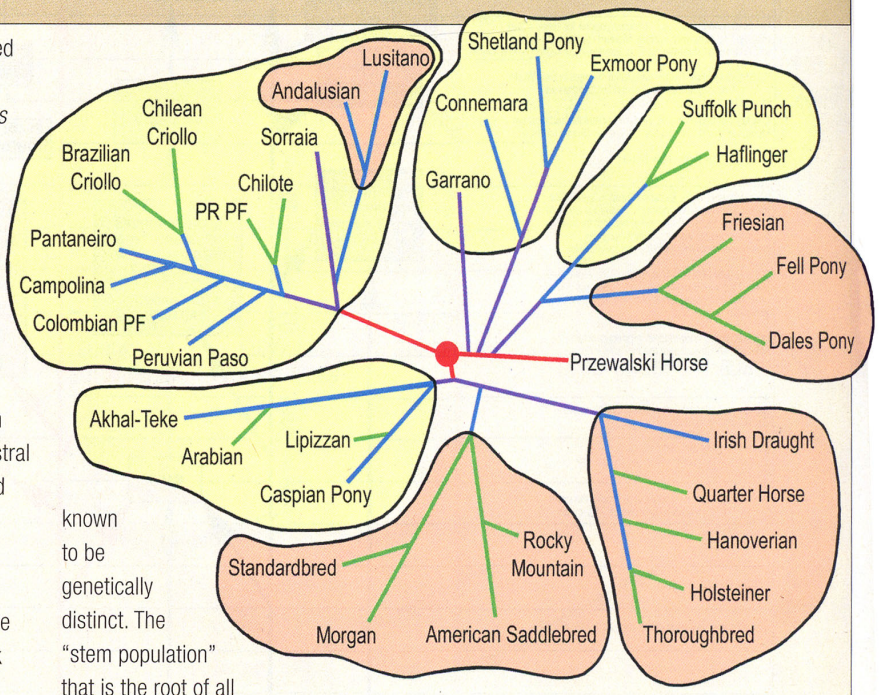
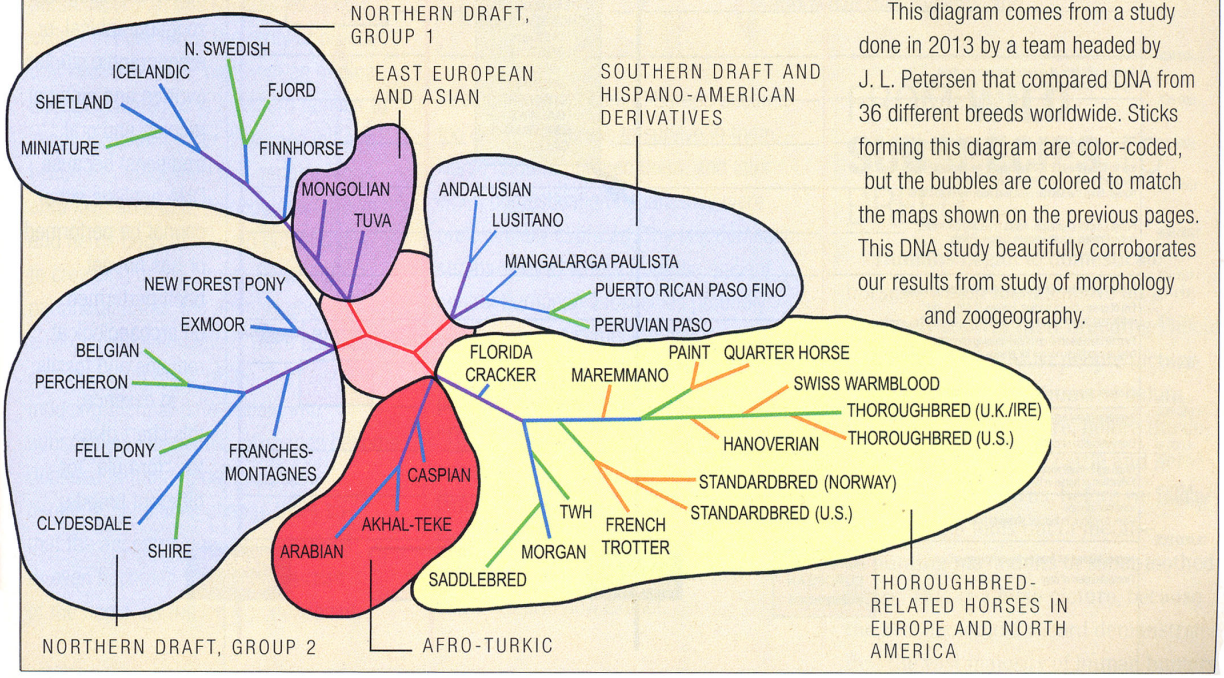
THIS IS THE SECOND HALF OF "THE ORIGIN OF HORSE BREEDS" (by Deb Bennett, Ph.D., 2014). TO OBTAIN THE FIRST HALF PLEASE CLICK ON THE APPROPRIATE .PDF BUTTON

GENETIC RELATIONSHIPS

This relationship diagram is modified from a 2007 study headed by C. Luis et al. published in *Animal Genetics* that focused primarily upon DNA similarities in Iberian-related horses. Bubbles in this chart are colored to indicate "intensity" of relationship, with either more loci or more frequent genetic matches equaling greater intensity. I have color-coded the sticks that form the diagram to show what morphologists call "differentiation events"—the points at which an ancestral population splits into branches, the end points of which are various breeds as they appear today. At least four orders of differentiation are necessary to derive all the breeds shown here; five are needed for the more inclusive work represented below. The Luis team's study utilized the Przewalski Horse as an "outgroup"—a comparison bloodline known to be genetically distinct. The "stem population" that is the root of all subsequent differentiation is not the Przewalski Horse but the Central European horse of the Pleistocene, *Equus caballus mosbachensis*.





This diagram comes from a study done in 2013 by a team headed by J. L. Petersen that compared DNA from 36 different breeds worldwide. Sticks forming this diagram are color-coded, but the bubbles are colored to match the maps shown on the previous pages. This DNA study beautifully corroborates our results from study of morphology and zoogeography.

from “The Origin of Horse Breeds” 2014 by Deb Bennett, Ph.D.
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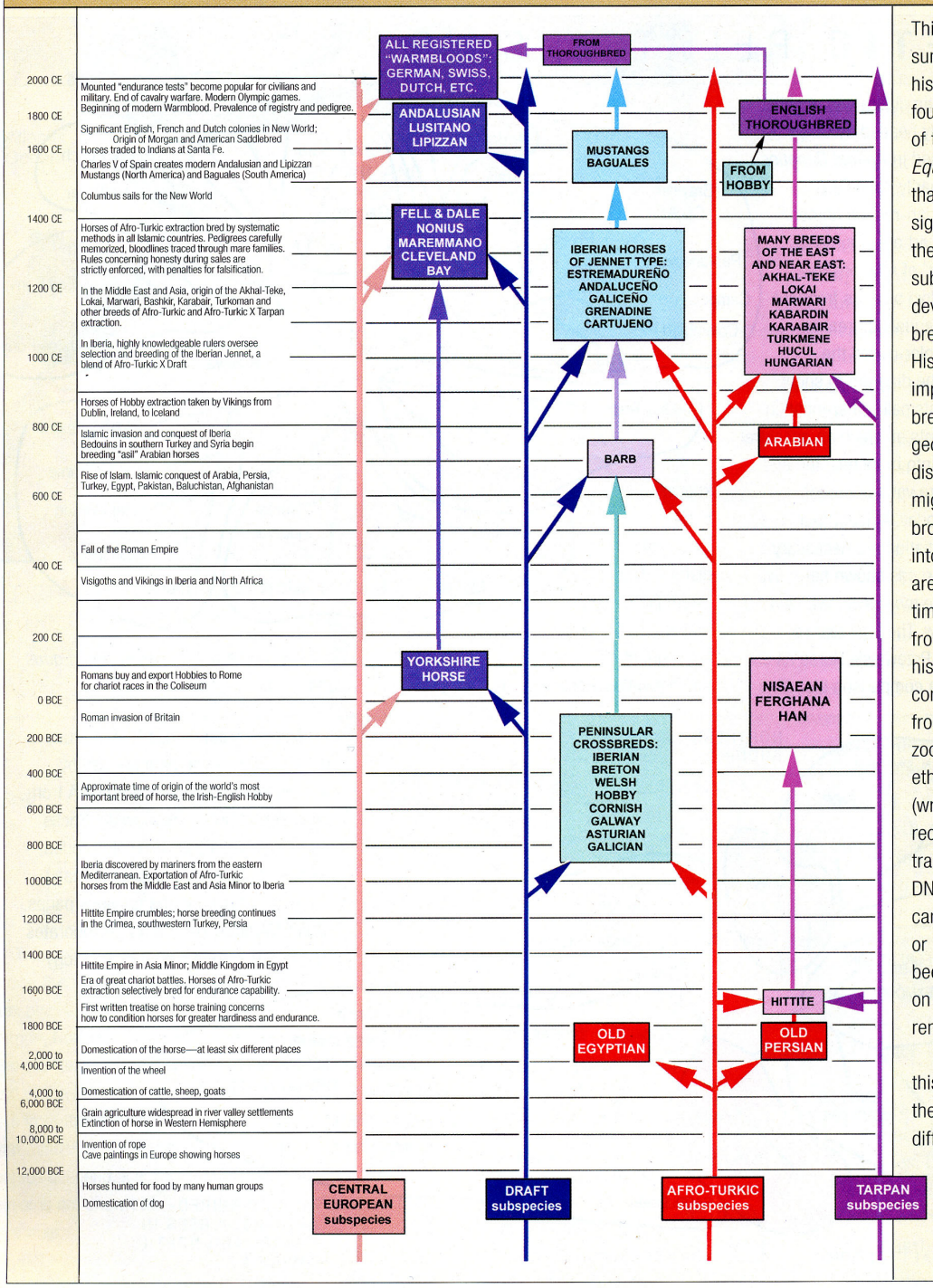

This chart summarizes the history of the four subspecies of the species *Equus caballus* that contributed significantly to the origin and subsequent development of living breeds of horse. Historical events that impacted horse-breeding, especially geographic discoveries or migrations that brought horses into new territories, are given on the timeline. Information from earlier historical periods comes primarily from morphological, zoogeographical, or ethnographic studies (written and pictorial records and oral traditions) because DNA analysis either cannot be performed or has not yet been performed on archaeological remains and fossils.

In essence, this chart gives the “formula” for different breeds,

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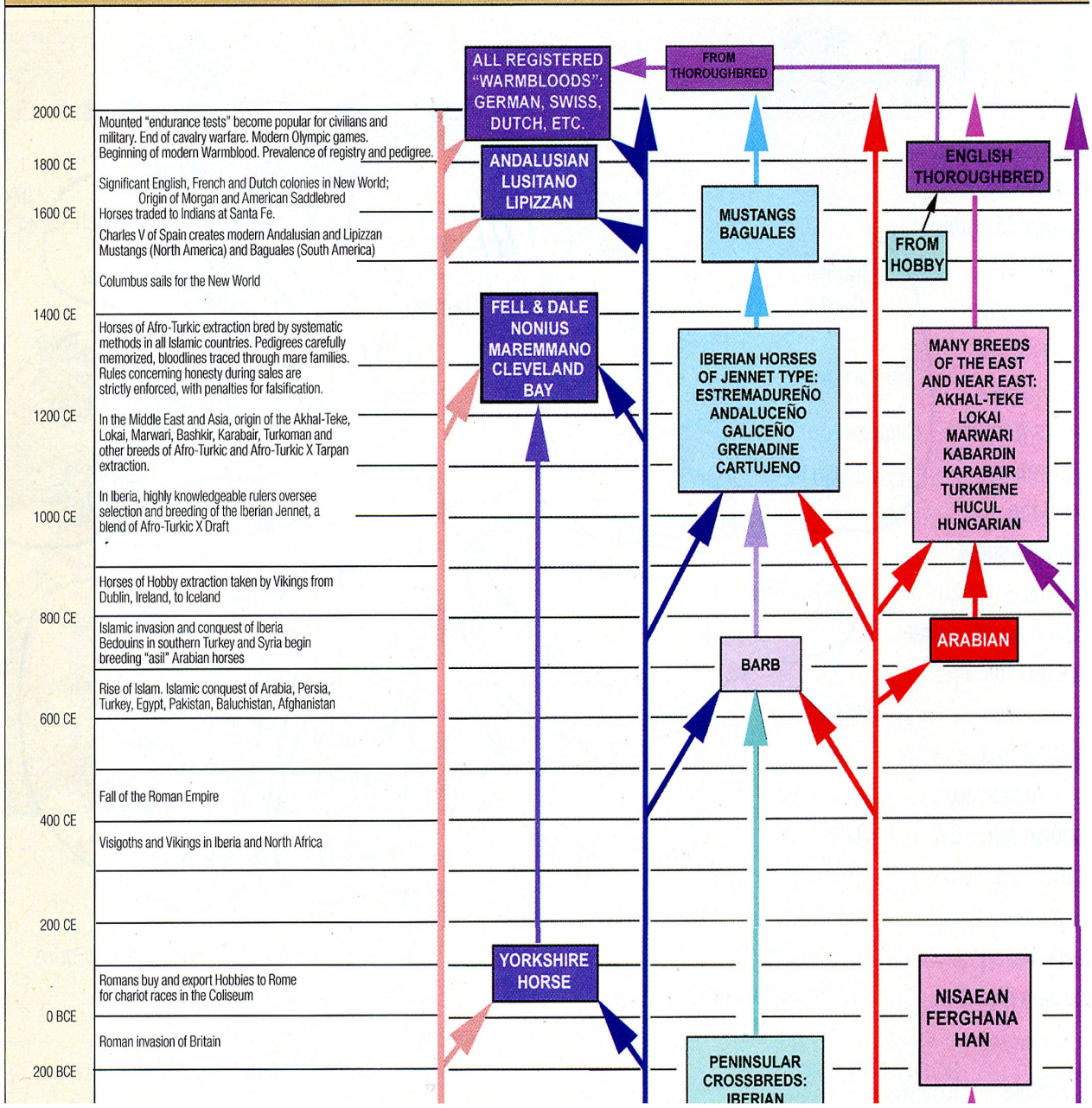
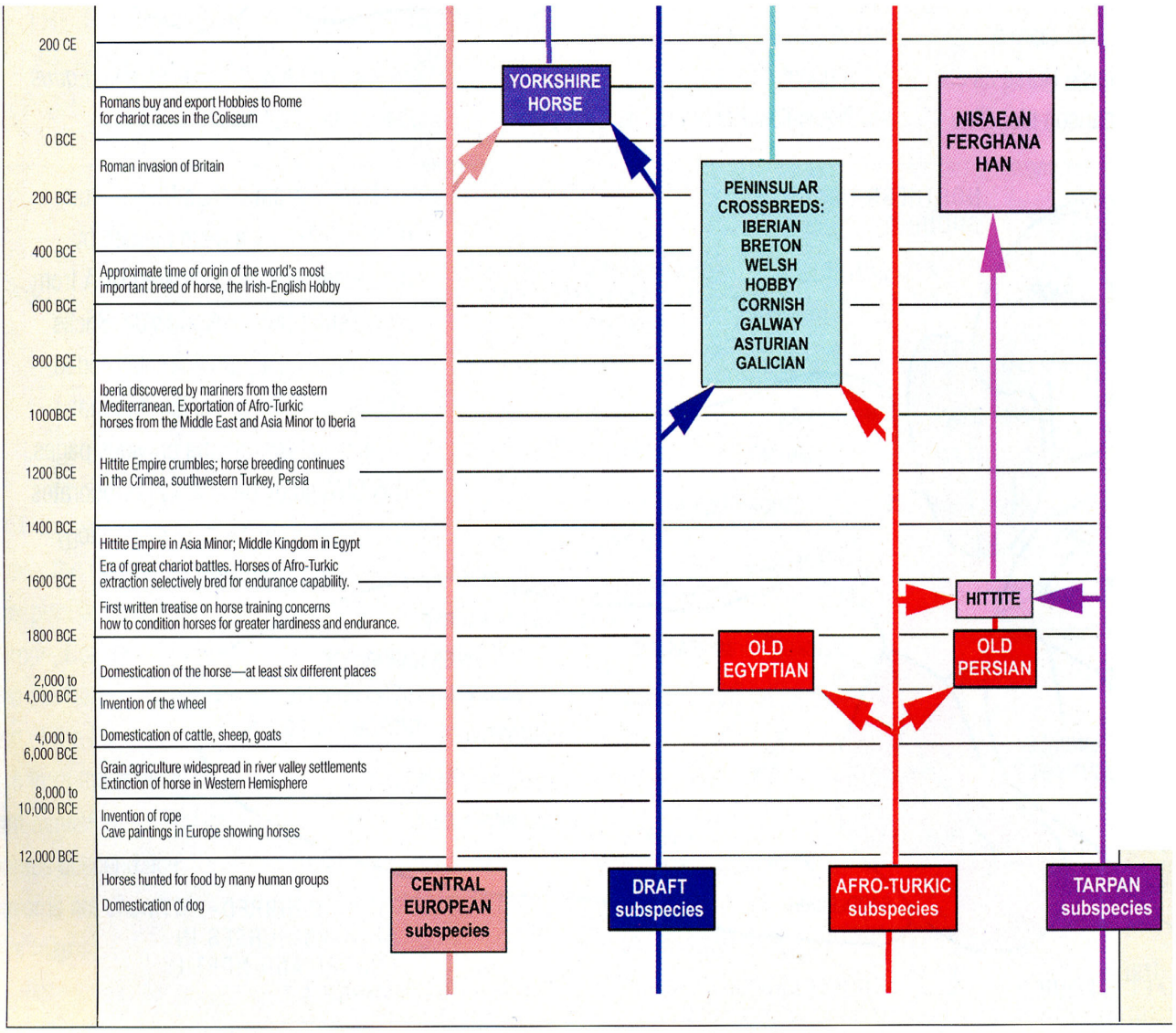
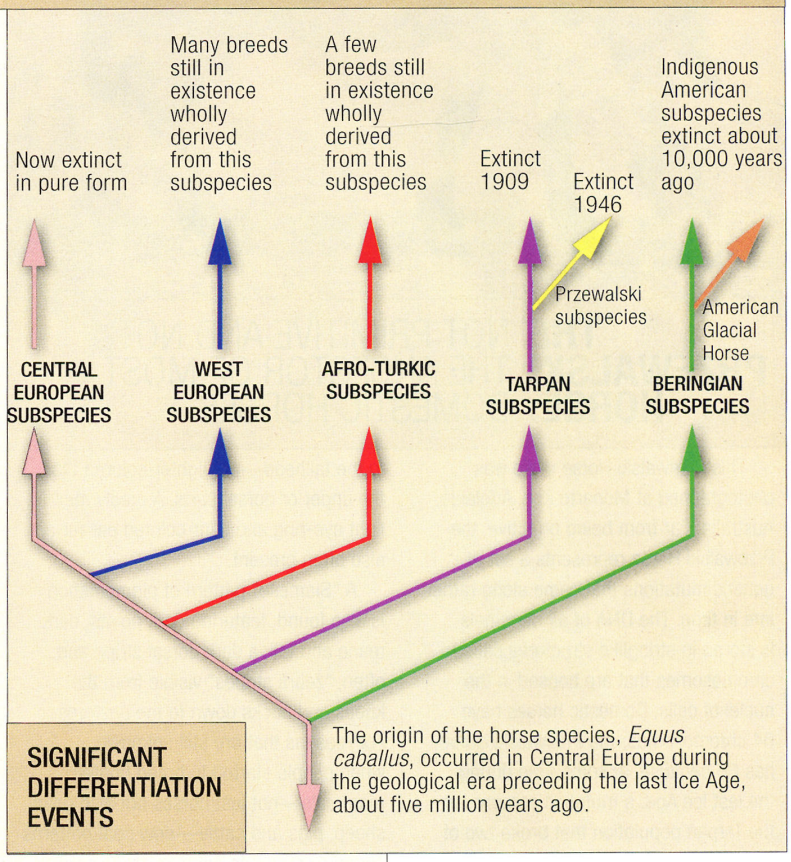


Bottom half of chart on p. 58



so that, for example, if all Thoroughbreds were to go extinct tomorrow, we could theoretically reconstitute a similar "Neo-Thoroughbred" by obtaining bloodstock from the appropriate root populations, which can still be found in less-populated or more remote regions of Europe and Asia. This teaches a very important lesson: Un-papered, non-registered, traditionally-bred, "countrified" horses have incalculable value. Every effort should be made to preserve many different strains, for they are treasure houses of the very genetic diversity that is the greatest hope we have for maintaining good temperament, tractability, hardiness and soundness in "purebred"—which inevitably means inbred—domestic bloodlines.

The chart at right shows the antiquity of the central European horse subspecies, which gave rise to all other horse subspecies and ultimately to all breeds of horse. Note that this subspecies is now extinct in pure form. The rarity of breeds that derive in major part from an original, central subspecies is a pattern familiar to zoogeographers. After a species initially becomes established in a geographic area favorable to it, its population grows and herds begin to spread outward due to crowding at the center. Reaching peripheral areas, the animals encounter environmental conditions more and more different from those of the "homeland," inducing them to differentiate into subspecies. Meanwhile, resources become depleted in the original geographic center or conditions change there so that the ancestral population declines or even becomes extinct. In the case of the horse, as the Ice Age deepened, forested areas in central Europe became too dense for horses to survive in them. Horse hunters pursued them, and later when domestication began, they were preferentially captured. The last domestic strains derived wholly from the ancient central European subspecies probably became extinct sometime between the World Wars, so that we can no longer point directly to any living horse and say, "This is an unadulterated example of the ancestral type." This, too, is a phenomenon familiar to zoogeographers and breed historians; the subspecies directly ancestral to dogs, sheep, goats and cattle are also now extinct.



FROM **WILD SUBSPECIES** TO BREED

Humans began to domesticate horses—which means above all to deliberately control their breeding—about 6,000 years ago. Most people picture "cave men"—that is, humans before the dawn of agriculture, before the domestication of sheep, cattle and horses, before the first towns, before we learned how to make tools out of metal—as hunting mastodons or saber-toothed tigers. This is a false picture, because the archaeological record demonstrates that the vast majority of human hunters

THE PRZEWALSKI HORSE: NOT PRIMITIVE AND NOT THE ANCESTOR OF MOST DOMESTIC HORSES

This Przewalski Horse mare was photographed at Monarto Zoo, Adelaide, Australia. Far from being primitive, the Przewalski Horse represents a set of genetic mutations that came along rather late in time. The DNA of all mammals is stored in stringlike structures called chromosomes that are housed in the nuclei of cells. Domestic horses have 64 chromosomes; the Przewalski Horse has 66 because, at some time during the last Ice Age, a mutation occurred in the Tarpan population that broke two of the chromosomes in half, creating a new profile numbering 66. The Przewalski Horse is thus not the ancestor but rather an offshoot of the Tarpan subspecies, which was itself an offshoot of an original horse population occupying Central Europe.

While its erect mane distinguishes the Przewalski Horse from domestic horses and their ancestors, the sandy coat color and the pattern of pigmentation are in fact primitive and thus observable in a wide array of horse bloodlines. The most characteristic feature of primitive coloration is that the animal's venter—the front of the neck, the underside of the belly, the flanks and inner gaskins, and the rear part of the thighs from the hocks up to the tailhead—are lighter-colored than the upper or dorsal parts. A mealy muzzle, light eye-ring and light-colored ear fur are also often present.

A "Siamese" pattern of pigmentation is also found, featuring dark points, dark mane and tail, a dark dorsal stripe and, often, "zebra stripes" visible from the knees and hocks down to the pasterns. For reasons that are still unknown, when people started to breed hoofed mammals—not just horses but also goats, sheep, pigs and cattle—new coat patterns suddenly began to appear. The first was the darkening of the venter to match, or more nearly match, the dorsum, as we see in bay or chestnut horses. Among wild mammals, this pattern is extremely rare. Another new pattern that emerged as a result of human-directed breeding was spotting—the various Appaloosa patterns and also all the many varieties of piebald, skewbald, pinto, splash-white, sabino, etc. Human choice also probably favored genes that cause the mane to grow longer, so that it falls down the side of the neck instead of more or less standing up, as it apparently did in the Ice Age Tarpan, Central European and West European subspecies that are the direct ancestors of living domestic horses.

across Europe and Asia specialized in killing horses. Horsemeat to the native European was as important as buffalo meat to the American Indian.

Humans had been hunting horses for 50,000 years or more before somebody figured out, between 10,000 and 6,000 years ago, that capturing them, breeding them, and riding them might actually be a better idea. When that momentous concept finally took root, everything concerning the horse species changed forever. When people imposed breeding choices on captive horses, they immediately began to affect conformation, not only creating preferred skull shapes but many other body features, such as high withers,

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which make horses better able to stand up to riding and driving. We also began to select for tractable temperament and "way of going," particularly the knack for ambling gaits versus the preference to "square trot."

All horse breeds originate from captured individuals that had been members of some wild subspecies. Archaeological research—as well as DNA studies—have shown that horses were domesticated at least six different times in separate places across Eurasia. This proves that, shortly after the idea and the techniques for capturing and breeding horses took root, the word—but not the domesticated herds themselves—began to get around. The first

REPRESENTATIVES OF SOME **OLD BLOODLINES**

Native to Galicia in northern Spain and northern Portugal, the Garrano is representative of a group also including the Asturcón (from Asturias) and Galiceños (from Galicia) which originated from the cover of mares native to the West European subspecies by stallions of the Afro-Turkic subspecies that were brought west from the eastern Mediterranean by Phoenician traders. These breeds are also important as once having been much more widespread within Iberia; they are the likely ancestors of many horses brought to the New World by Spanish and Portuguese explorers and conquistadors. (photo by Maria Lemos)

The Exmoor is native to the British Isles and representative of the northern population of the West European subspecies. During the coldest phases of the Pleistocene, so much of the world's water was frozen into ice that sea levels were lowered several hundred feet. This caused the English Channel to partially dry up and provided a land-bridge by which horses could migrate from continental Europe to Britain. Ice cover of the British landmass was also extensive during the coldest periods, meaning that horses could live only in the southern parts of the main British island. During warmer intervals, the ice margin temporarily retreated, permitting horses to migrate northward but also raising sea levels, which stranded them on the island. (photo by Menthedogs)

Native to southwestern Spain and southern Portugal, the Sorraia is representative of the southern population of the West European subspecies. Iberia contains one of Europe's two great grasslands, and it apparently served as a refugium during the last Ice Age, where horses found good conditions for survival. Despite its coloration, which resembles that of the Przewalski Horse, the Sorraia is no more "primitive" than any other strain of domestic horse. No strain of American mustang descends from the Sorraia, despite frequent advertising claims that are based mostly on the fact that the coat color and pattern are similar. Coat coloration in horses is never, in itself, good evidence for close relationship. (photo by Hardy Oelke)

Some old bloodlines, continued ....

These Pantaneiro mares are native to the Pantanal, a zone of tropical wetland bordered by dry tropical forest in southern Brazil. The Pantaneiro represents a survival of the commonest type of horse imported during the American conquest. Once arrived in the New World, these horses found conditions very much to their liking, and a population explosion occurred during which domestic herds escaped to become feral. Horseflesh free for the taking then converted many native tribes to a mounted and nomadic way of life. Like the Uruguayan and Argentinian criollos, the Llanero of Venezuela, and the horses of rural Bolivia, Paraguay, Nicaragua and El Salvador, the Pantaneiro has been brought back from the brink of extinction by dedicated and knowledgeable fanciers who found remnant populations surviving in remote areas or in the hands of Indians. Note the similarity in conformation to the Garrano—this is what the horse of Spanish Estremadura and Andalucia once looked like; they are the "Andaluceños" of the 15th and 16th centuries. (photos courtesy, Gus Cothran, PhD)

The Chilote is one of several island-remnant strains to be found in both North and South America. This, too, is an animal of a type similar to that originally exported from Estremadura and Andalucía. After the European invasions of various countries of the Western Hemisphere during the late 15th and early 16th centuries, within 50 to 100 years there ensued in many areas a colonial era of generally peaceful prosperity. During this period the importation of horses from Europe slowed to a trickle or entirely stopped, because American horse populations increased so greatly that importation was neither necessary nor economical. As colonies prospered, roads began to be improved while horse breeders endeavored to improve their stock by careful selection. "Countrified" horses of the original bloodstock—the common term is "petizo" in Spanish—became more and more marginalized; people did not want them grazing fields in competition with cattle. Petizos were then driven or shipped to offshore islands as an inexpensive means of fencing them in, with roundups held annually to keep population numbers low enough to balance available graze. The size of the horses decreased in response to limited island resources. This is the history of the Chilote—a priceless antique left over from the conquest of Chile. (photo courtesy, Gus Cothran, PhD)

The Friesian probably carries a greater contribution from the ancient Central European subspecies than any other living breed. Like most "warmbloods," the Friesian has in the past been crossed with draft horses, Thoroughbreds and other breeds. It has also gone through population declines that create "genetic bottlenecks" when almost all surviving horses descend from only a few stallions. Nonetheless, the Friesian continues to give us a good idea of the appearance of the most ancient of all the subspecies of *Equus caballus*.

group of people to domesticate horses probably lived in what is now southern Russia, but not long afterward we find evidence for horse domestication in Iberia, Western Europe and West Asia. A glance at the zoogeographic maps shows that horses captured by people living so far apart must have belonged to different wild subspecies.

Long-distance transport of horses took thousands of years to develop. When shipping became possible at around 1100 B.C., people began to move stallions from the Middle East west across the Mediterranean, giving impetus to matings that would never have occurred without human intervention. Foals resulting from the cover of mares native to western France, northern Iberia and the British Isles by stallions of West Asian and Middle Eastern origin were an important early example of within-species hybridization—the interbreeding of animals from widely separated subspecies. This is why Robert Hoffmann and I were particularly interested in mapping the distribution of different horse subspecies at the end of the last Ice Age, about 10,000 years ago—because this was the last moment in Earth history at which all members of the species *Equus caballus* were still wild animals, the last moment when the map would show the distribution of natural variation in bone and body shape.

STRANGE BEDFELLOWS: DNA AND MORPHOLOGY STUDIES

The relationship between morphology, zoogeography and DNA studies has been a somewhat uneasy one because the traditional way of classifying animals is by observable characteristics, yet the relationship between these features and particular genes remains, even today, obscure and difficult to elucidate. Despite the current popular fascination with DNA—largely driven by television shows with "CSI" in the title—genetic studies cannot do everything. Presently, no researcher can say with certainty which gene or group of genes determines most physical features in horses, dogs, humans or other higher vertebrates. Morphology studies thus remain crucial to "fingering the culprit," so to speak, because without them we would just have a cheek swab or a blood sample, which cannot tell us whether the culprit was 13, 35 or 80, muscular or skinny, covered with tattoos or with a scar on his forehead, spoke with an accent, had a full head of hair or was as bald as an egg.

It has been particularly problematic to come up with a purely morphological definition of "breed" because often the identification we seek is from skeletal remains that are thousands of years old, so that characteristics such as the fineness or the color of the coat, length of the ears, way of going, longevity, temperament or hardiness that are used to identify many horse breeds cannot be brought into play.

At the opposite extreme, anytime we equate a breed with the modern club or registry that keeps track of pedigrees and which may also function to promote the breed for sale, we have left the realm of biology. Even with its enormous power to clarify blood relationships, DNA taken from ancient horse bones cannot be used to "assign" the remains to any modern horse breed, because ancient remains date from long before the sires and dams who, by registry rules, constitute the "foundation" of the breed. Probably the best solution to this conundrum is to shift the discussion from "breeds" to "bloodlines," which are historical continuums.

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While it is tempting to view DNA and morphology/zoogeography studies as being somehow opposed, the correct and more positive view is that they are complementary. You can't have a CSI show without the quirky medic who works down in the morgue or upstairs in the pathology lab: He's a morphologist and a necessary part of the team.

The very fact that the techniques used for DNA analysis are completely different than the techniques used to detect, describe and interpret body-shape lends special power to parallel studies. When results agree, it constitutes powerful evidence that conclusions are accurate. When DNA results are at variance with what the morphologist perceives, that's the moment when Our Hero, the famous crime-lab detective, steps in and really begins going to work, because some important piece of evidence, some crucial bit of data, has clearly been missed.

Happily, zoogeographic maps, ancient artwork, historical research, morphology studies and DNA studies on the horse largely agree. Rare is the popular horse magazine that will print real data, as EQUUS has always done; and rarer still is the opportunity for a single contributor to report 26 years of scientific progress. In our next installment, we'll begin our survey by looking at one of the world's oldest and most important horse breeds—the Arabian. There are some surprises in store even around this well-known breed, so dear reader, hold onto your hat while the equine adventure begins—again."

EQUUS thanks Ernest (Gus) Cothran, Jr., PhD, of Texas A&M University for his contributions to the research for this article as well as its preparation.