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TRACING THE “GAIT KEEPER” GENE

Recent scientific studies have shown that the knack for lateral-limb coordination—the ability to pace—is genetically determined. In about a dozen breeds from around the world, the responsible allele (a mutation called DMRT3-STOP which has been nicknamed the “gait-keeper” allele) is present in virtually every horse. In the lingo of geneticists, this means that this allele is “fixed” in the population.

In many other breeds the allele is not fixed, yet as many as three-quarters of tested individuals may be carriers. The “wild type” or normal gene sequence encodes a transcription factor that plays an important role in the fetal development of spinal cord circuits that control limb movement. The DMRT3-STOP allele blocks formation of this factor, which in turn permits lateral-limb coordination.

The DMRT3-STOP mutation has

Researchers continue to learn more about how horses inherit the ability to perform so-called lateral gaits that make them easy to ride.

By Deb Bennett, PhD

significant effects upon a horse’s athletic capabilities in addition to permitting lateral-limb coordination. First, it allows carriers to move at high speed in either trot or amble. As the world map shows, the DMRT3-STOP mutation occurs at low frequency in non-gaited breeds, and studies suggest that this is probably due to selection against this variant by breeders. DMRT3-STOP carriers may

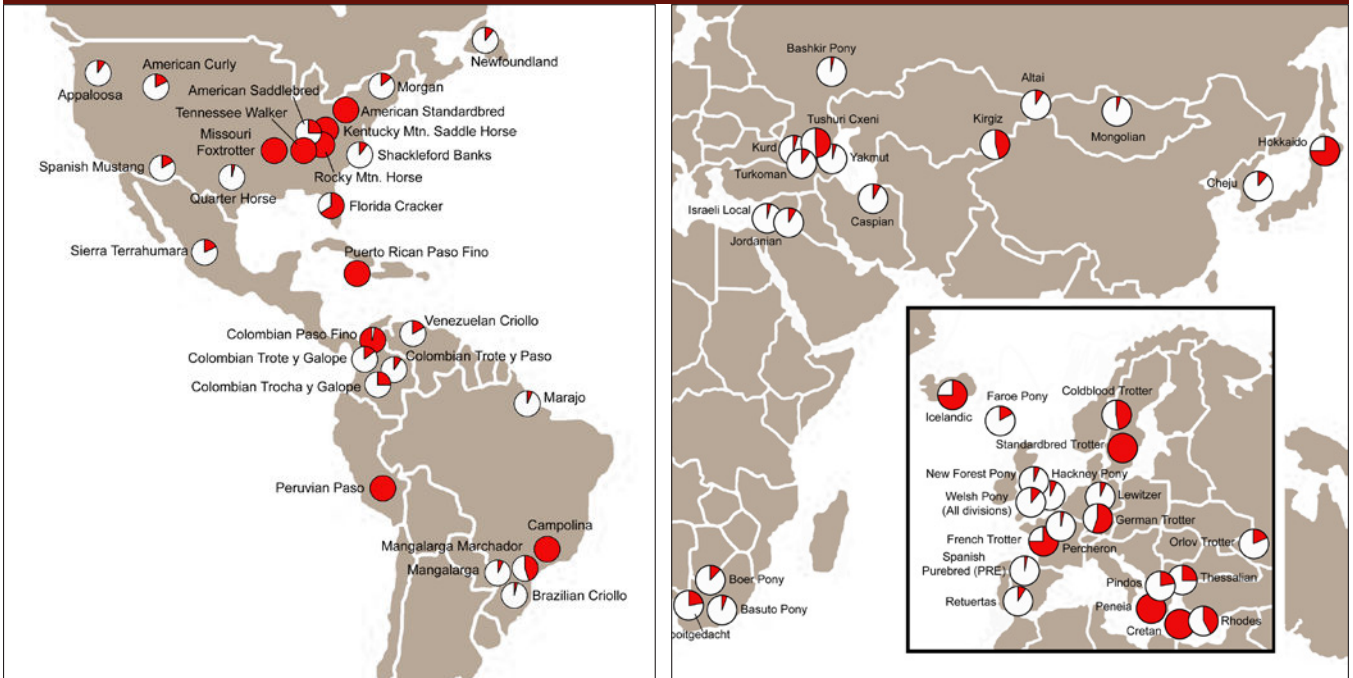
be “mixy gaited,” which can make them appear clumsy when they attempt to canter. Further, when asked to increase speed, they may prefer to continue in a four-beat lateral coordination rather than switch to the diagonally coordinated canter. In racing breeds, selection against DMRT3-STOP has been intense because while the mutation enhances speed at the trot and pace, it inhibits it at the gallop.

How Old is the responsible Allele?

In 1984 researcher Elise Renders published an analysis of a fossilized trackway from Africa attributed to the now-extinct three-toed horse genus *Hipparion*. Her study surprised me and a lot of other biologists and horsemen because it clearly showed that the animals crossed a muddy beach at moderate speed, not at a walk or trot but at an amble. Although there is no way

GEOGRAPHIC DISTRIBUTION OF THE “GAIT KEEPER” GENE

World maps showing selected ambling and non-ambling breeds. Red indicates the percentage of individuals tested who carry the DMRT3-STOP gene (data after Staiger et al., 2017).



to prove it, it is tempting to assume that DMRT3-STOP was the factor allowing the Hipparion adults and foals who made the hoofprints to locomote in this way. Because the African trackway is some three-and-a-half million years old, it is also tempting to assume that we’ve all had it backwards: that the normal mode of locomotion in the taxonomic Family Equidae involves lateral rather than diagonal coordination of the limbs.

There are, however, several telling arguments against this idea. Surveys of gene structure in a wide array of species show that the wild-type allele which favors diagonal-limb coordination is the normal allele found in all mammals and indeed in all vertebrates. Przewalski horses are not ancestral to domestic horses, but they have not been selected for either racing ability or for “easy” gaits and thus comprise an excellent

comparative population. In a 2014 study, Maria Promerova and colleagues found that all tested Przewalski horses were homozygous for the wild type.

A follow-up study in 2017 by E. A. Staiger and colleagues confirmed that DMRT3-STOP is absent in Przewalski horses and is present in less than 50 percent of unselected feral horses such as the American Spanish Mustang and the Mexican Sierra Tarahumara. Their study brackets the origin of the mutation in the species *Equus caballus* at between 467 and 9,595 years ago, with the most likely time being about 4,000 years ago—in other words, shortly after the horse became domesticated. This is more than three million years later than the Hipparion trackway, and therefore if DMRT3-STOP is the causative factor, it must have arisen independently in both species. This is entirely possible since the

difference between wild-type and mutant alleles involves the substitution of but a single base pair.

Further, a 2013 study by Ludovic Orlando and colleagues on mid-Pleistocene horse skeletal material from Alaska with DNA preserved by permafrost confirms the idea first proposed in the 1940s by vertebrate paleontologists that the lineage giving rise to all modern members of the genus *Equus* originated about 4.5 million years ago. This means that the genus *Equus* is much older than the Hipparion trackway. If DMRT3-STOP arose in *Equus caballus* only 4,000 years ago, the wild-type allele predominated throughout all but the last one percent of the history of this lineage. It is thus safe to conclude that in those domestic horse breeds where the DMRT3-STOP allele is found at high frequency, it has been selected for by breeders.



Artwork and written records suggest horses that can perform lateral gaits have been preferred throughout history.

Amblers in Antiquity: Eastern and Western Strains

An overwhelming amount of evidence, both in the form of artwork and from written records, suggests that ambling horses have been preferred throughout history by travellers. Not only are these horses comfortable to ride, they also require less riding skill or specialized techniques. As has been pointed out before, posting to the trot, which makes that gait bearable for distance riding, was not invented until the end of the 17th century and was not in wide use in Europe or the Americas for more than a century after that.

As Europe and western Asia emerged from the Neolithic into the Bronze Age, horses began to come into the hands of peoples whose homes lay south of the Silk Road. The natural range of the horse lies mostly north of this east-west line, and horses were domesticated and first used for riding by nomadic tribes living in the north. The southerners, living in the ancient kingdoms of Egypt,

Persia, Assyria, Syria and Babylon, began to acquire horses and the knowledge of how to capture, train, handle and ride them from the nomads around 3,500 years ago. Artwork, along with occasional written records from this very early period, prove that ambling horses were present throughout the Middle East from very early on.

As to the western strain, the importance of the now-extinct ambler-galloper English-Irish Hobby is clear. I have called Hobbies “the world’s most important horse breed,” yet they never show up in modern genetic studies. The reason is simple: The breed is now extinct in pure form. This skews the results of



such studies, which must always be evaluated with the understanding that the basic data is incomplete. Every other form of evidence that we have—artifacts, artwork, zoogeography, linguistic study and written document—trumpets the crucial contributions of the Hobby to both European and American horse breeding.

Horses called “hobby,” “obino,” “aubin,” “paso” or “palfrey” (the latter term derived from another old Latin word—“palaveri”—a name for ambling horses bred by a tribe of that name in Brittany) were present in England, Wales, Ireland, Scotland, northern Iberia, France, Germany and Italy from before the foundation of the Roman Empire to the beginning of the 19th century. Where we have records of the value of these horses, it is always much higher than the common farm horse or trotting “haquenée.”

In a recent ethnographic survey, historian Fabienne Meiers notes that in Pliny the Elder’s day—the Roman Empire of the first century A.D.—ambling horses intended for riding were bred mostly in the Celtic regions of Iberia, specifically Asturias, and were considered luxury goods. Pliny says that Asturian horses “moved both legs on the same side alternately” and did not trot—indicating that the “gait keeper” mutation was already present in Europe more than 2,000 years ago.

There are thus two rather widely separated groups or strains of amblers whose history dates back to antiquity: a western Hobby strain, and an eastern strain. Which of these may be the older—or whether DMRT3-STOP may have arisen more than once independently within the species *Equus caballus*—is a question not yet resolved by geneticists, as it requires testing of archaeological remains with preserved DNA. ■