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The Evolution of The Horse

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In the most basic sense, evolution means change. Evolution is a very dynamic process, full of twists, transitions and dead-ends (i.e. extinctions.) Evolution is the result of genetic adaptation to environmental changes combined with a great deal of luck and opportunism. From a mammalian perspective, the mass extinction of dinosaurs (65 millions years ago) was a lucky event as it opened a new opportunity for the expansion of mammals.

In this brief overview of the horse's evolution, I chose to highlight a few landmark horses that are not the result of a straight lineage of evolution. I will also focus somewhat on the morphological and biomechanical changes of the lower limbs.

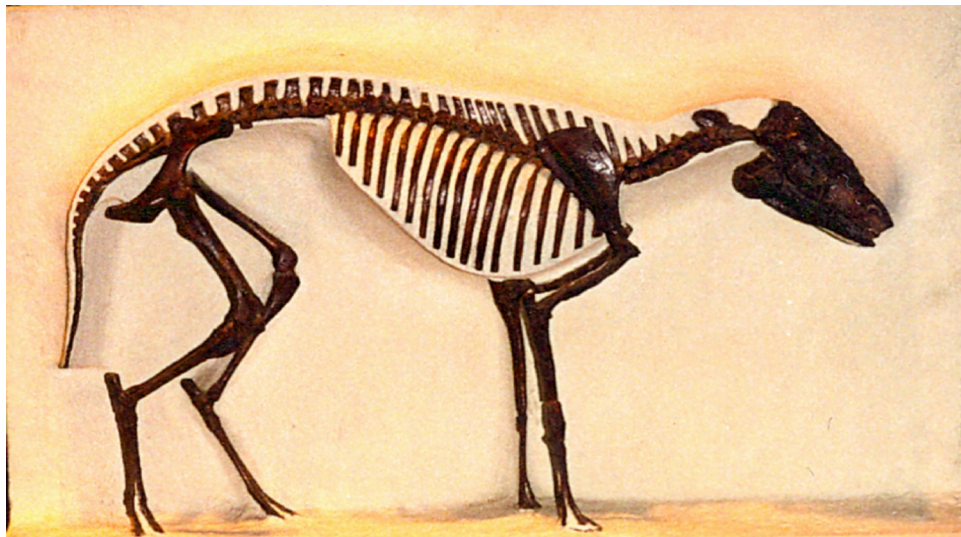


Figure 1: Hyracotherium, an ancestor of today's horse.
Image courtesy of Pamela J. W. Gore, Georgia Perimeter College.

The first direct ancestors to modern mammals appeared during the Eocene (55 – 33 million years ago (mya)), such as horses, tapirs,

rhinoceros, camels, hippopotamuses and pigs. At that time, the global climate was generally warm and mild. The 'seasons' as we know them today did not exist. The continents were not yet in their current positions. At one point in time (circa 200 mya) all the continents were lumped in one mega continent called Pangea. By early Eocene, the super continent Laurasia (what is now Europe, Asia, North America and Greenland) broke up and sent North America and Greenland drifting further apart from Europe and Asia. The island continent of India was 'floating' at sea on a collision course with Asia. It is in this environment that the earliest horse ancestor – hyracotherium - made its debut (Figure 1.) The fossils of these creatures were found in Europe, Asia, and the Canadian Arctic. Compared to the modern horse, hyracotherium was a small animal the size of a house cat or small dog (circa 10 inches tall.) It had an arched back, short neck and legs and a narrow muzzle. Hyracotherium was a regular browser. His diet consisted of mainly leafy vegetation, i.e. shrub leaves and plants, not grass. Hyracotherium's stance was that of a digitigrade -- an animal that walks on padded toes. This creature had four toes in the front and three in the hind. Hyracotherium's stance and skeletal structure did not allow for high speed nor spring-like gaits. It is very likely that hyracotherium was moving more like a modern tapir than a modern horse.

By early Oligocene (33 to 24 mya) the global climate was cooler and drier. The continents continued to drift apart. Oceans continued to cool. This global cooling affected plant and animal life. Forests gradually yielded to woodlands and open lands. The first tridactyl (having three toes) horse appeared during the Oligocene. Meshippus had three toes in the front and hind limbs. All toes had pads. Meshippus was a browser and stood about 20 to 24 inches high.

The Miocene epoch (24 to 5.3 mya) was a time of extensive mountain building. The Himalayas, the Rockies and Andes rose

up. This epoch marked the start of global cooling. Antarctica, Greenland and the North Pole began to have large glaciers. The chimpanzee and hominid lines split in the late Miocene. Oceans receded during the Miocene. This allowed land mammals to disperse between Eurasian and African continents.

The Miocene saw the largest diversification of horse species and saw the most significant morphological changes in horses. The Miocene saw at least three different groups of early horses. These groups lived simultaneously during the middle and late Miocene. One primitive group called the Anchitheres. The animals retained their tridactyl padded foot and were browsers. The Anchitheres became extinct by late Miocene.

The second group is that of more advanced tridactyl horses. These horses were grazers, meaning they ate grass. They were the first horses that displayed spring-footed locomotion. The central toe of these horses became significantly larger and became the primary weight bearing structure, while the lateral toes diminished in size and function. It has been speculated that the lateral toes touched the ground only when these horses were at a running walk. The first landmark horse in the second group appeared 17 millions years ago and goes by the name of merychippus. This horse would be recognizable by today's standards. It stood about 10 to 12 hands tall. Merychippus had long legs, a long face and was the first grazing horse. This animal was found throughout North America.

The third group contained monodactyl (having one toe) horses such as pliohippus and dinohippus. Both horses appeared in middle Miocene and lived to late Miocene. Pliohippus and dinohippus are recognized as mostly monodactyl. The lateral toes disappeared gradually in some species but remained in others. These horses probably went through gradual transitional stages of evolution rather than abrupt splitting. Fossils of pliohippus were

found in Colorado, the Great Plains and Canada and those of *dinohippus* were found throughout North America.

During the Pliocene (5.3 – 1.8 mya), the continents finally attained their present day positions. The cooling and drying trend continued during this era. In the higher latitudes, cool weather plants (lichens and mosses) grew on frozen tundra. Deciduous and coniferous forests were found in slightly lower latitudes. Tropical forests and plants were limited to areas around the Equator. Dry savannah and deserts appeared in Asia and Africa. Many land mammals looked like modern mammals. The first human like primates appeared in East Africa during the early Pliocene. *Equus* also made its debut during the early Pliocene. *Equus* was the first species of all modern horses. These horses were small and stocky, having the height of a medium pony (circa 12 to 13 hands.) Compared to the late Miocene monodactyl horses, *Equus* had a more advanced stay apparatus. The stay apparatus is a system that allows horses to lock their joints in the fore- and hind limbs in order to conserve muscular energy while standing. The Pliocene saw a reduction in horse diversity.

The Pleistocene (1.8 – 0.011 mya) is often referred as the Great Ice Age. Artic glaciers expanded and retracted cyclically over Europe and Northern America. The earliest modern humans appeared in Africa 200,000 years ago. Modern humans started to disperse in earnest from Africa throughout the world around 70,000 years ago. Early Pleistocene marks last era of significant mammal diversity. This era was also the last time that horses lived in North and South America. By late Pleistocene, a huge number of large herbivores went extinct, followed by carnivores and scavengers. Climate fluctuations, the advent of man and possibly diseases are the main reasons for this mass extinction. In North America, horses and other large herbivores along with saber-toothed tigers and giant wolves went extinct by late Pleistocene, only a thousand years

after the first appearance of humans on this continent. Horses did not go extinct in Eurasia and Africa.

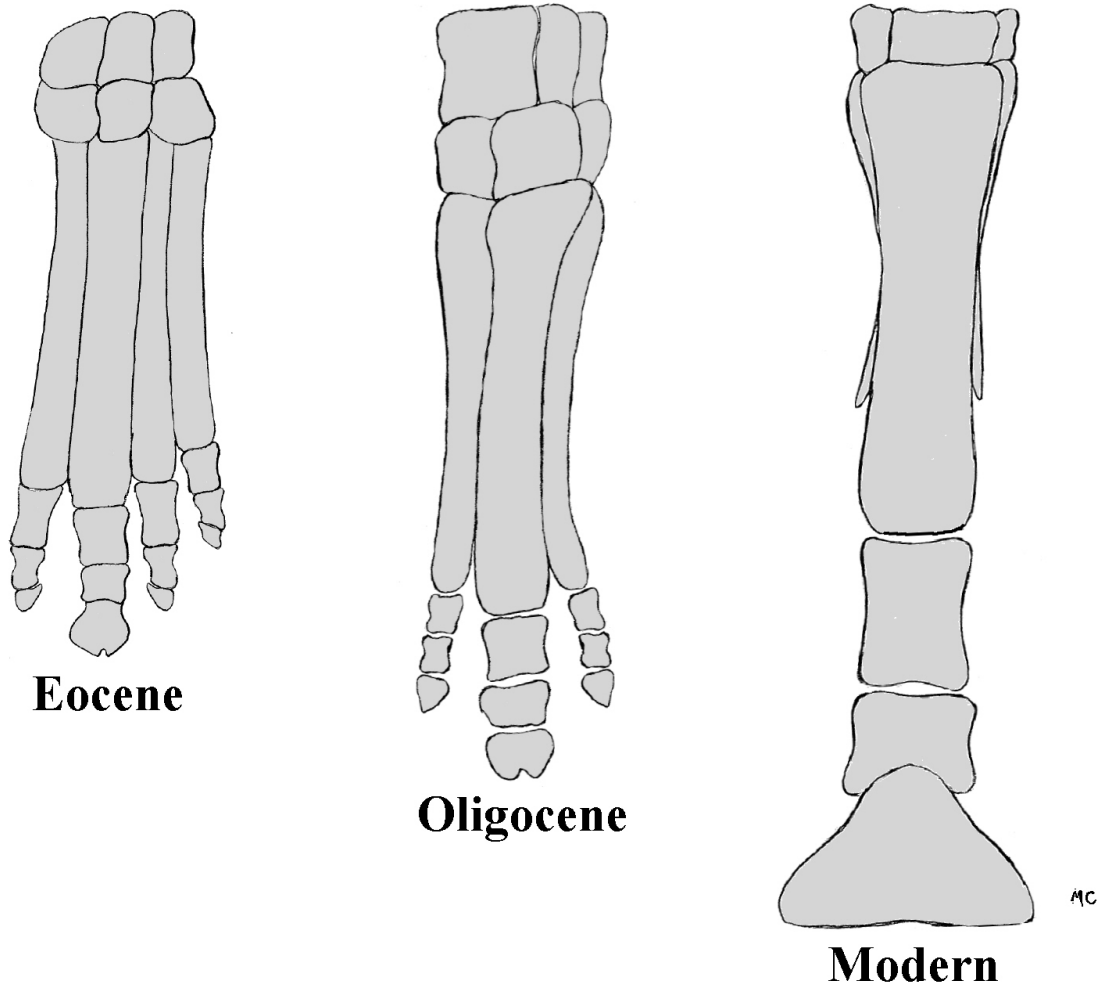


Figure 2: Evolution of the lower limb of the horse. The outer two phalanges present in the Oligocene limb have degenerated to the 'splint bones' of today's horse.

The Holocene epoch (10,000 years ago to today) starts right after the last cycle of Pleistocene glaciation. The main event of this current epoch is the rise of human civilization and its impact upon our planet. The later part of the Holocene marks the start of a perturbing trend towards the ecological collapse of the earth due to human activity. In the early Holocene, the horse was hunted for

meat. Although there are some debates on what exactly consists unequivocal domestication, it seems the horse was domesticated around 5000 years ago in Central Asia. At that time the sole purpose of the horse was to provide milk, meat and carry loads. Horses were not the first animals to be domesticated by men. The wolf, about 12,000 years ago, sheep, goats, cattle around 9000 to 7000 BC, cats around 3000 BC.

The ancient horse was a fairly slow moving browser, whereas today's horse is a fast moving grazing animal. The ancient horse lived mostly in a forest environment where protective hiding places were numerous, and speed was not crucial. As the horse evolved, it came to live mostly in more open grasslands. In open grasslands, speed enabled the horse to flee from predators. Anatomical changes in the biomechanics of the limbs occurred as part of the evolution of the modern horse as a direct consequence of the change of environment (Figure 2.) Important evolutionary adaptations can be seen in the stance of the limb, along with numerous details having to do with ligaments, tendons, and muscles. Muscles connect to the bones via tendons; this is true in the ancient horse as well as the modern horse. The muscle and tendon arrangement and their mechanical properties make the difference between the ancient slower moving browser and the modern galloping horse. When we take a more detailed look at tendons, we find variation in their length and energy-storing abilities. In the case of muscles, we find different types of muscles, and some muscles are called semi-tendonous because they seem to be a hybrid between muscles and tendons. Generally, tendons and ligaments are of great importance in the locomotion of fast, springy-legged animals. Tendons have the ability, like springs, to store a tremendous amount of energy, and to return it to the biomechanical system very quickly. Arrangements of tendons, ligaments, and bones can store and release energy and do this very quickly. Muscles work on a slightly slower timescale because of the need for significant neurological interaction. The brain must

tell a muscle to contract, and time is needed for this processing; a tendon or ligament acts on its own as a spring, without needing to consult the brain.

Fossil records of the horse show changes away from muscles and towards a greater involvement of tendons and ligaments. In one such case, a muscle called the interosseous muscle, found in the lower limb in ancient horses, has disappeared in the modern horse, leaving only a ligament. This, and other changes moved the horse from motion dominated by simple muscle action, to today's motion that has a higher reliance on tendon and ligament action.

In today's horse, we have an animal that runs on a single digit. The major muscles are found high in the limb, with only tendons and ligaments in the lower limb. In such an animal, damage to a tendon (or unnecessary surgery) has a great impact on the survivability of the animal.

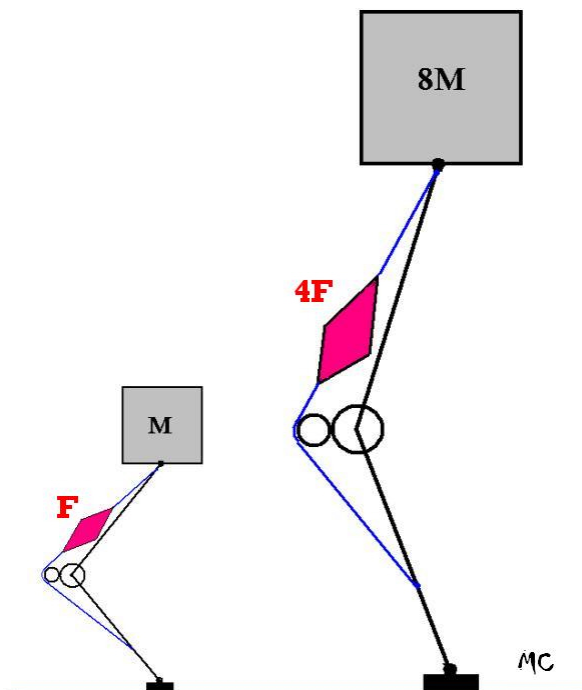


Figure 3: Roughly speaking, an animal that is twice as big in lineal dimension has 8 times the mass, but only 4 times the muscle strength. Therefore, it must stand with a more upright posture.

Another change over time is that the horse became larger. The increasing weight of the animal has had implications on the limbs and the horse's stance. In general, larger animals stand more "up right" than smaller animals. Hyracotherium was small and stood on somewhat crouched legs. Today's larger horses stand on legs that are fairly upright. This comes from a biomechanical necessity – as animals get larger, their weight goes up faster than the strength of their muscles (Figure 3). To compensate for lack of muscle strength, the animal must stand more erect because this improves the mechanical advantage at the joint, requiring less joint torque from the muscles (try standing in a half-squat for a long period of time, and you will soon notice the increased muscle activity required). Smaller, lighter animals can stand crouched because their weight to muscle strength ratio is lower.



Figure 4: The horse's foot (A), the dog's foot (B), and the foot of the tapir (C). The frog and digital cushion of the horse is a descendant of the pad found in other animal's feet.

Tapir image courtesy of Patricia Medici.

If you have looked at a cat or dog paw, you have seen that they walk on ‘pads’ (Figure 4). Technically the modern horse is no longer a padded animal, but it displays remnants of a pad in the form of the frog and digital cushion. This back part of the horse’s foot still functions like a pad in many respects. As evolution proceeded, the original nail or claw developed into the hoof capsule. Receptors that sense pressure and vibration (called ‘pacinian corpuscles’) can still be found in the caudal area (back part) of the hoof (Figure 5). These receptors are commonly found in skin (human skin, the pads on dog’s feet, etc.) These receptors sense vibration and pressure applied to the surrounding structures. Their presence is another indication that the rear portion of the hoof is related to pads in other animals.

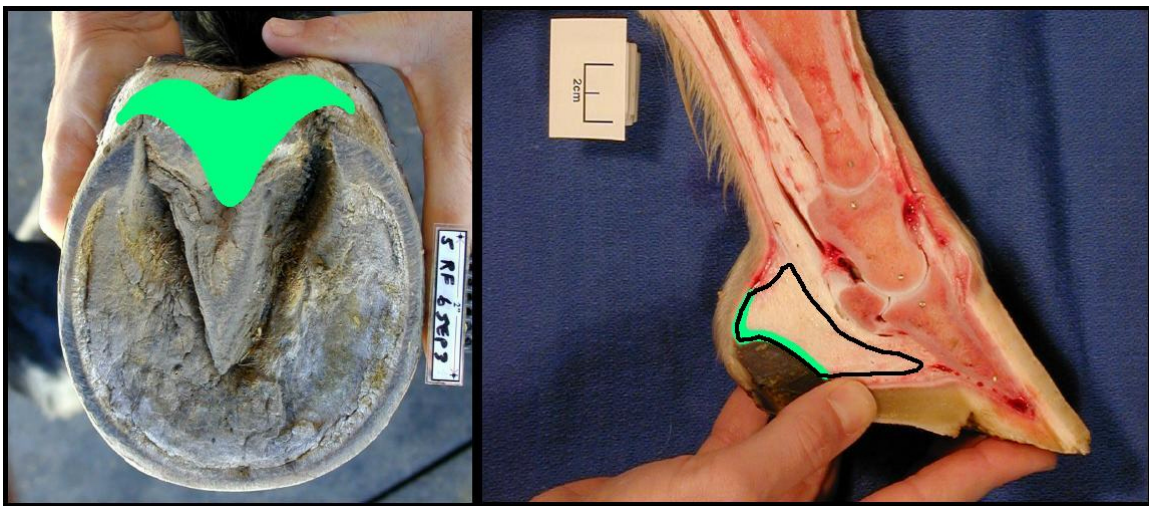


Figure 5: The area in green shows where pressure receptors are found in the hoof. The digital cushion is within the region indicated by the black line in the right-hand image.

Each time I pick up a horse hoof, it reminds me the long evolutionary time that was required to create this miracle of engineering. The horse is well designed for its position on the tree of life!