

THE EVOLUTION OF THE HORSE FAMILY



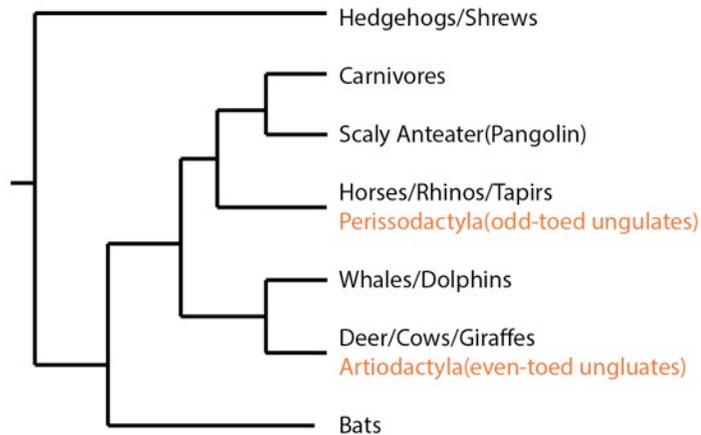
by Michelle Tribble

The Horse family has been a classic example of evolution for scientists for nearly 160 years. Our beloved horse has been the subject of tireless research in seeking evidence for evolutionary theory. What was once portrayed as a streamlined linear example of evolution from an early horse form to the modern horse form has expanded to a diverse and sporadic evolutionary picture. Since the earliest discovery of the prehistoric tiny horse relatives to the modern science of paleontology, we continue to modify and update our knowledge of the evolution and family tree of the horse. Dr. Bruce J. MacFadden stated in his essay *Fossil Horses - Evidence for Evolution* the dissolution of linear evolution theory in horses:

Since the early 20th century...paleontologists have understood that the pattern of horse evolution is a more complex tree with numerous "side branches", some leading to extinct species and others leading to the species closely related to *Equus*. This branched family tree is no longer explained in terms of predestined improvements, but rather in terms of random genomic variations, natural selection, and long-term phenotypic changes. (MacFadden, 2005)

The genus *Equus* is no longer considered the end goal of equine evolution, but rather the lone survivor on one end of the elaborate bush of the diverse Equidae. "The family tree of horses enjoys exceptional popularity and is widely accepted as fact" (Franzen, 2010 p.100).

SUPERORDER LAURASIATHERIA



NEW GENETIC PHYLOGENY, SOURCE: *Trends in Ecology and Evolution*. 19: 430-438

Equines

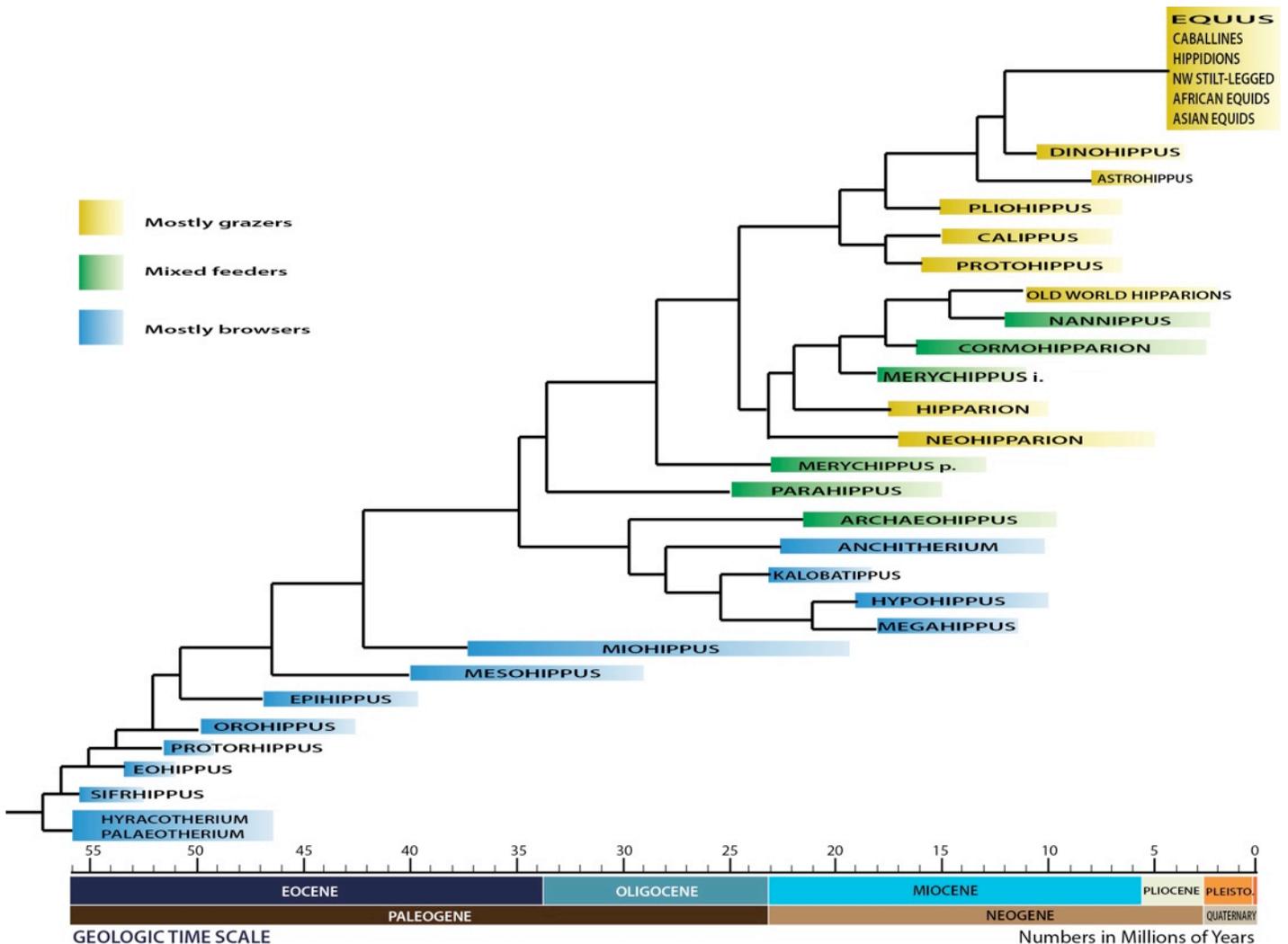
The horse family, Equidae, is a family within the Order Perissodactyla (the odd-toed ungulates), which includes the families of rhinoceroses and tapirs. An ungulate is a mammal that is considered to walk around on its tip-toes, or hooves. The Perissodactyls began evolving and diversifying during the early Eocene epoch, around 55 million years ago, as any earlier fossils have yet to be discovered. Equidae has only one extant (living) genus, *Equus*, with seven species, and numerous subspecies. The seven species groups are African Wild Asses (Donkeys), Horses (domestic and wild), Grevy's Zebras, Onagers, Kiangs, Plains Zebras, and Mountain Zebras. Species and subspecies of *Equus* can interbreed and form hybrids. There are approximately 35 other genera, all extinct, within the family Equidae. The above diagram shows the horses' closest relatives, within the mammal superorder Laurasiatheria.

Horses are large herbivorous mammals that have long slender legs ending in a single toe covered by a horny hoof. They have adapted to surviving in open plains, deserts, and mountains. They are a social animal that prefer to live in large herds. Horses are built for speed and running long distances; they are the only other mammal besides humans that can produce large amounts of sweat for thermoregulation. Equines are primarily grazers but can eat fruits and leaves when needed. They have large grinding molars to chew fibrous grasses. They have specialized digestion, and are not like cows and other ruminants that use multiple stomach compartments and re-chew their food. Along with other even-toed ungulates, they use a large caecum ("hindgut") in their colon for digesting their high cellulose diet (Franzen, p. 12-17).

The Horse Family Tree

In the world of taxonomy, the science of classification, fossil horses have provided an amazing wealth of evidence, and also the problem of where to put them all in relation to each other. Countless fossil specimens have emerged, species have been identified, named and renamed, classified and reclassified. The history of the horse family has been updated many times, and undoubtedly will be continuously revised as we gain understanding into this vast fossil record.

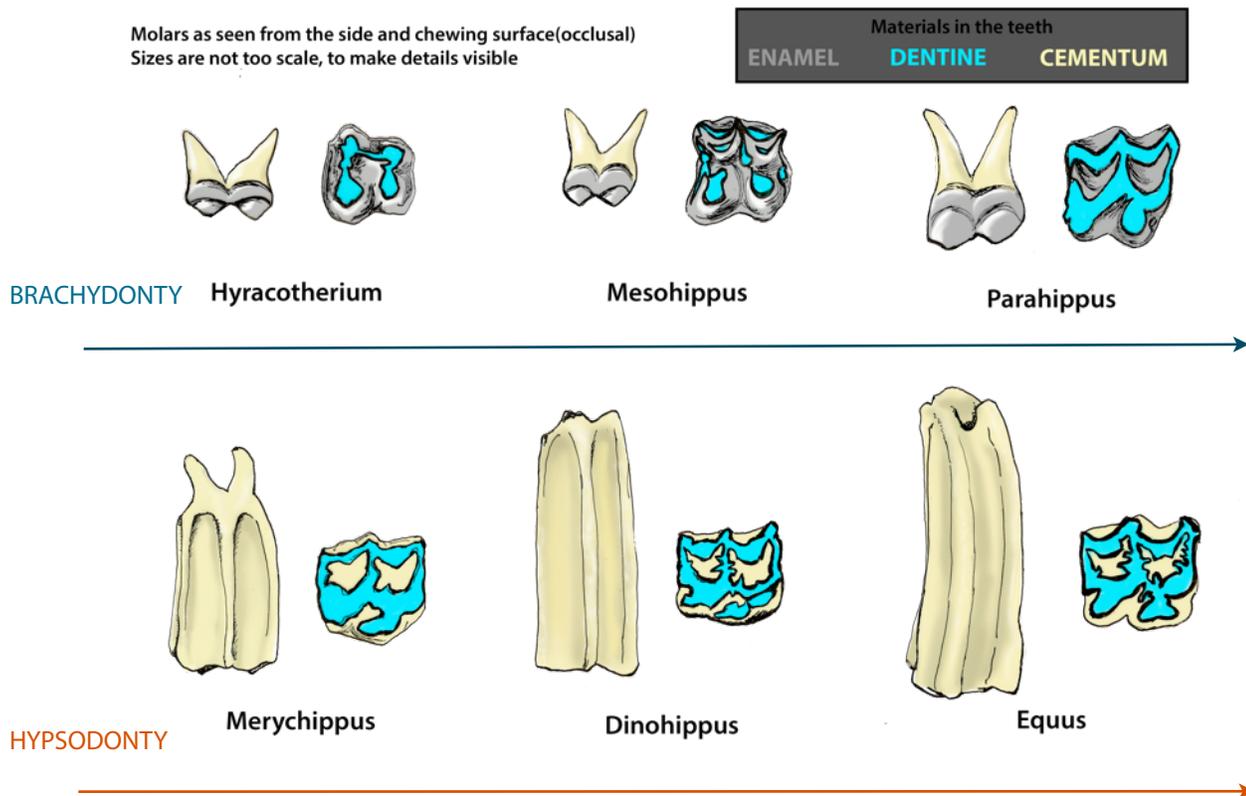
With advancements in molecular technology, scientists are able to study further into the genetic relationships of varying equine species, using current and ancient DNA. Still, a highly debatable picture is presented when it comes to the phylogeny of horses. The graph below is a lineage of common genera. With continued research and technological progress, we will develop better insight into these amazing animals and their incredible evolution.



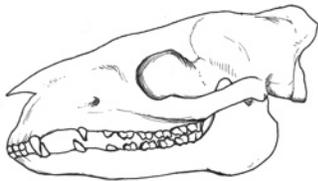
Phylogeny of the Horse Family. Adapted from MacFadden 2005, Mihlbacher 2011, Froehlich 1999, Weinstock 2005.

Dietary Change Revealed in Teeth

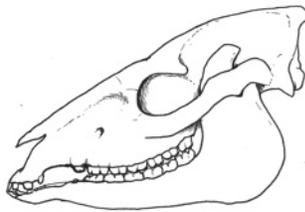
Today's equids are well adapted to grazing on a diet of tough grasses, and the dirt they can pick up with that. Horses have molars, or "cheek teeth", that are high-crowned(tall). This is termed hypsodonty(hypso meaning "height" + donty meaning "tooth"). The molars are also deep-rooted and covered in cementum(hard, bony substance) rather than softer enamel. It's sometimes hard to imagine that they came from tiny fruit-eating ancestors, that had small bumpy low-crowned molars. Around the mid-Oligocene the climate began to grow increasingly arid and forests began to give way to grasslands. Horses began consuming more grasses and slowly ventured out into the savannas where they could keep a better eye out for predators. The chewing(occlusal) surface of the molars also began to change from a smooth bumpy surface for fruit diets, to a sharp shearing surface for leaf-browsing, to a blunted complex surface for grinding. There were periodic reversals and trends in the teeth of equids, but eventually what we are left with is the trend towards hypsodonty(Mihlbacher, 2011).



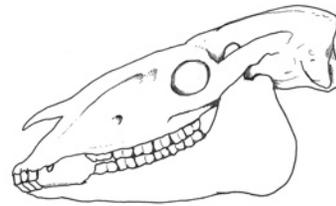
HYRACOTHERIUM



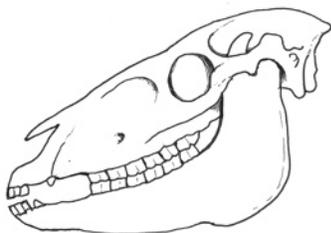
MESOHIPPUS



PARAHIPPUS



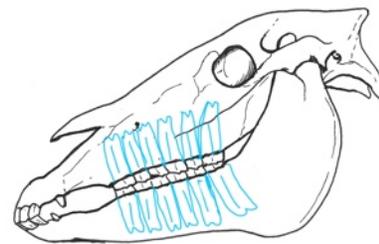
MERYCHIPPUS



DINOhippus



EQUUS



Sizes are not to scale, to make details visible

Interior inset of teeth in skull

Structural Adaptation

Why did the horse lose its side toes in the course of evolution? Over fifty-five million years the horse progressively reduced the side toes and reinforced the middle ray of the foot. There are obvious limitations to being reduced to a single toe covered by a hard hoof, and having legs with limited side rotation, but the development of such highly specialized feet gave the horse many advantages. The rhinoceros and tapir, although closely related, did not lose their first and third toe, but they are also not built like the horse: tall, lithe and fast. Monodactyl (one-toed) horses are best on hard, solid-ground surfaces, as opposed to soft or spongy forest floors. Earlier horses, such as *Mesohippus*, would use all three toes to support its weight and did not have the necessary structure to conserve energy for standing for long periods of time. Later horses developed a reinforced tendon and ligament structure for better stabilization, an energy-saving "stay-apparatus", and their extra digits became vestigial (Franzen, p.85). All that remains of three-toed horse, presently, are two "splint" bones on either side of the cannon (lower leg) bone. Horses still retain the genes for these extra toes and have been known to, very rarely, be born polydactyl (multiple toes) (Ewart, 1894).

As these specialized runners developed their feet, we also see big evolutionary changes in body size, leg length, skull depth, and brain size. Scientists used to think that horses evolved continuously from small to large, but we know through fossil evidence that is not entirely true. Ancient horses had two "size" phases, the first phase from 55 to 20 million years ago when they remained around

HYRACOTHERIUM



MESOHIPPUS



PARAHIPPUS



MERYCHIPPUS



DINOHIPPIUS



EQUUS



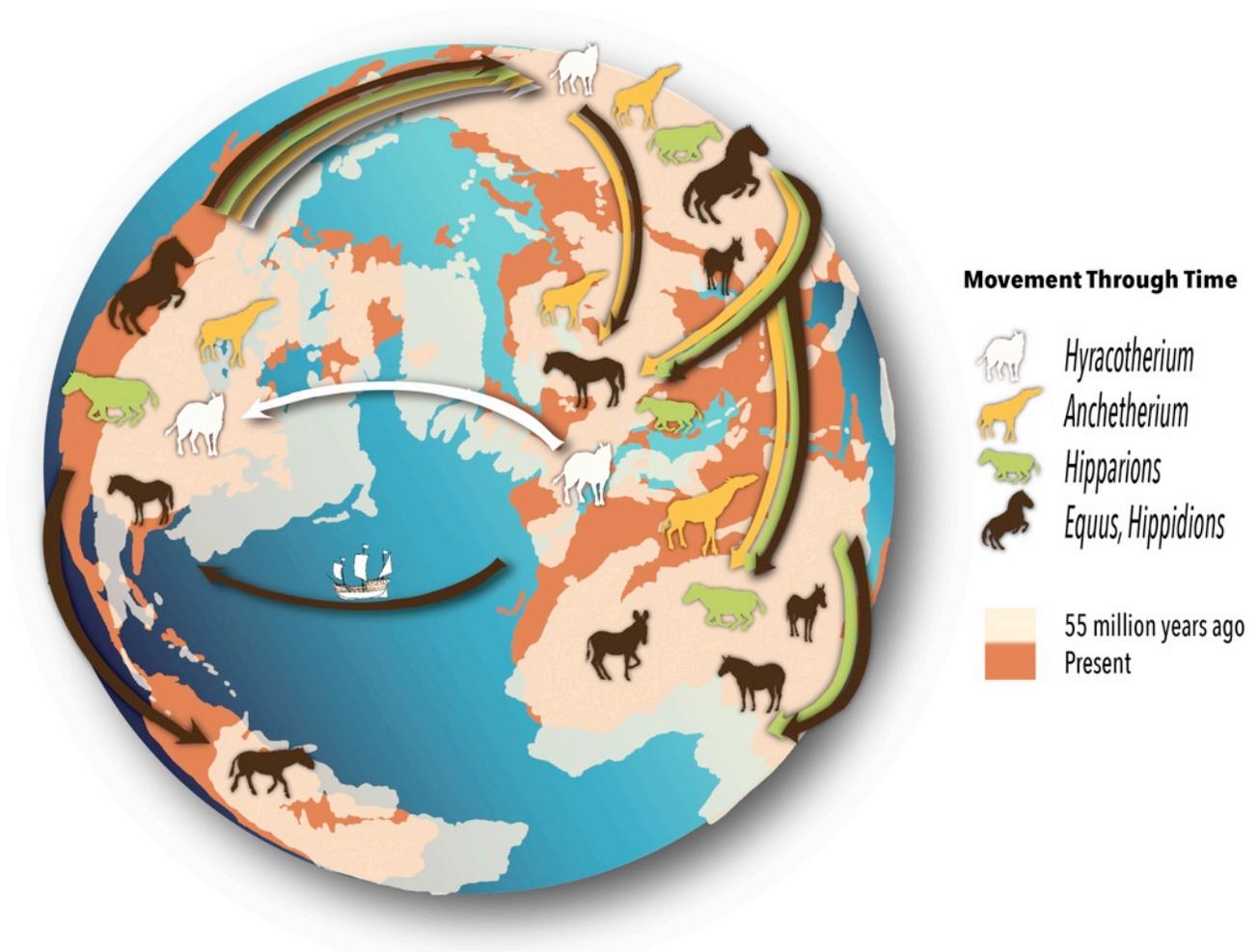
Sizes are not to scale, to make details visible

10-50 kg; and the second phase from 20 million years to present when horses became very diverse in their sizes, some clades(groups) even shrunk in body size (MacFadden, 2005). The clades that became larger in size(modern horses can be around 500 kg) gave rise to the surviving genera. Is there an advantage in evolving into larger sizes? In *The Rise of Horses*, by Jens Franzen, he states "the metabolism of larger organisms is more economical than smaller ones," meaning you conserve energy better the bigger you are. But the strength of the organism's musculature needs to correspond with the size, and either an organism tends to get very large and slow, and specialize in defense(against predators), or they get tall with specialized locomotion. For example, elephants are too big for most predators to stand a chance, and horses have natural predators, but have the speed and endurance to usually outlast their attackers(Franzen, p.92-93).

Expansion of Equidae

The movements of the horses around the globe is very interesting as an organism's evolution is highly impacted by it's environment. The fossils of the earliest known horse ancestors, the *Hyracotherium*, were found in Europe. Ancestors earlier than *Hyracotherium* may have come from Africa and migrated to Europe during a faunal exchange in the early Eocene. But no direct fossil ancestors have been found. The European *Hyracotherium* probably crossed into North America via land bridges 55 million years ago, and then isolated evolution of the horses began(Franzen, p.118).

After millions of years in North America, horses returned to the Old World via the land bridge that connected Alaska and Siberia which formed around 40 million years ago, and periodically opened and closed until the end of the last ice age. Once in Siberia, horse genera could migrate across Asia, and into connecting continents of Europe and Africa. Horses also moved into South America when the continent connected to Central America around 3 million years ago. And after domestication by humans in Eurasia, equines finally returned to the Americas in 1493, in ships with the Spanish invasion (Franzen, p. 182). Australia and New Zealand were eventually inhabited by horses as well, when European immigrants brought them in 1788 (Franzen, p. 144). Below is a figure of the movement and expansion of the varying horse types.



Adapted from Franzen, 2010. Maps adapted from Colorado Plateau Geosystems, 2011.

Dawn Horses of Europe and North America

Hyracotherium



Hyracotherium, formerly known as *Eohippus* ("dawn horse"), is the earliest known genus of the horse family. The first fossil discovery was in 1839 in southeastern England. This small forest-dweller lived during the early Eocene, it averaged 20-40cm high at the shoulder - about the size of a small dog, and had an arched back. It had four padded toes on the rear feet, and three padded toes on the front feet. *Hyracotherium* had short-crowned (bracydonty) molars and were browsers of green leafy vegetation and fruit, and lived primarily in a tropical to subtropical climate (Franzen, p. 18). Current research has found that *Hyracotherium* does **not** belong to the family Equidae, but to another closely related family - the Palaeotheres, and is restricted to Europe (Froehlich, 1999). They still belong in the horse superfamily Equoidea, but not in the direct lineage of Equines. It is likely the *Hyracotherium* share a common ancestor with the other dawn horses. The early North American genera of *Eohippus* (the name has been resurrected), *Xenicohippus*, *Sifhippus* and *Protorohippus*, that were previously classified as *Hyracotherium*, belong in the earliest line of the Equidae (Norris et al., 2009).

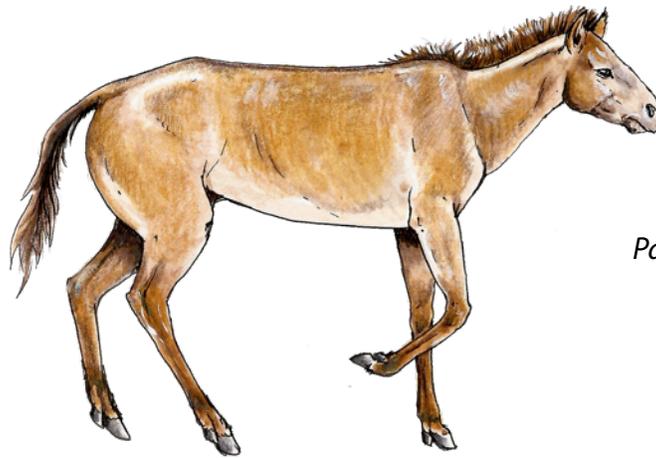
Early Horses of North America

After the evolution of the dawn horses several notable genera emerged and demonstrate significant transitional forms. "Equids evolved on [North America]... via *Orohippus* (Middle Eocene) and *Epihippus* (Late Eocene) into *Mesohippus* (Early Oligocene) and *Miohippus* (Late Oligocene)" (Franzen, p. 124). *Mesohippus* ("middle horse") was a common and successful small dog-sized horse, averaging 60cm tall at the shoulders (withers). Its molars were similar to earlier

Mesohippus



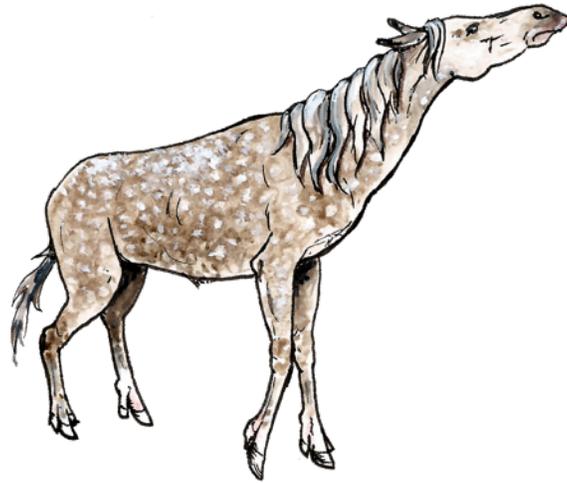
forms, low-crowned (brachydont) and conditioned to eat a mixture of tender leafy vegetation. *Mesohippus* had a slightly longer face, and a larger brain than its predecessors. *Mesohippus* had three toes on all four feet, with the center toe becoming more dominant in size (MacFadden et al., 1996).



Parahippus

Around the beginning of the Miocene the *Parahippus* developed from *Mesohippus*. The genus *Parahippus* exhibited transitional teeth, in-between a low-crowned molar for browsing and a high-crowned molar for grazing grass. This type of horse would have been a mixed browser, eating both soft vegetation and grasses, venturing out into grasslands. The climate is considered tropical to subtropical, and with a mixture of woodland and savanna vegetation. (MacFadden, 1994, p.285). *Parahippus* was larger, around 65cm tall at the withers, with a longer face. *Parahippus* was better developed for faster strides on open terrain. There was a greater reduction in size and use of the first and third toe on each foot, and it was able to stand (but not run) on its middle toe solely.

North American Horses Move into Eurasia



Anchitherium

Horses during the Miocene began to traverse the Bering Strait land bridge that connected North America and Asia. The first group of horses to do this were the subfamily *Anchitheriinae*. They were three-toed and low-crowned browsers. They spread throughout North America and into Eurasia. Genera from *Anchitherium*, despite remaining browsers, included the large *Megahippus* and *Sinohippus*.



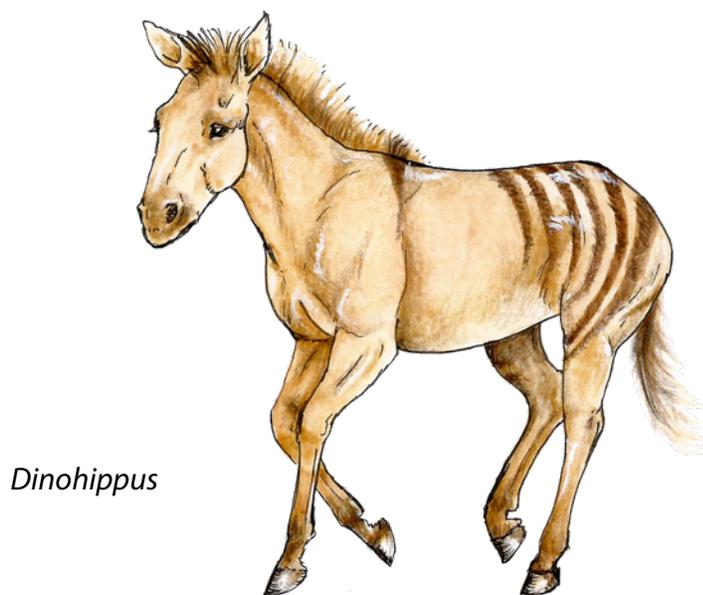
Merychippus

Merychippus followed *Parahippus* in the long line of horse lineage during the middle Miocene. *Merychippus* was a diverse genus with many species and groups that stemmed from it. It was a three-toed horse and was adapted to sprinting fast, and in some species its side toes were smaller, only touching the ground during running. It began to resemble the modern day horse, with a longer face, and was pony-sized. *Merychippus* was truly a grazer, “*Merychippus* is characterized by increasing high-crowned (hypsodont) cheek teeth with a very complex chewing surface (occlusal pattern)” (Franzen, p. 124).

Equines Spread into Africa

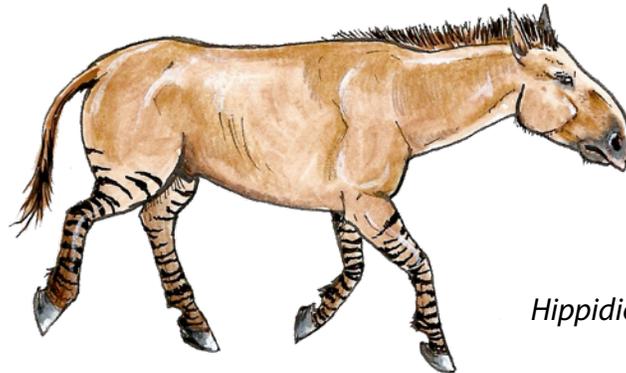


One group that descended from *Merychippus*, besides the modern horse, were the three-toed *Hipparions*. This group of horses were very successful with many genera and species, and widespread, reaching all the way into Africa (South America was still isolated at this time). They lived through the Miocene and Pliocene and varied in size, even producing the dwarfed *Nannippus*.



Dinohippus (name meaning "terrible horse") emerged 11 million years ago in the late Miocene, and survived into the middle Pliocene. *Dinohippus* is a direct ancestor of the living equines. It is considered an intermediate between middle Miocene genus *Pliohippus*, a descendant of *Merychippus*, and *Equus*. *Pliohippus* had demonstrated an increasing reduction of the extra digits. *Dinohippus* has been found both in three-toed and one-toed forms (MacFadden et al., 1996). It was roughly the size of a modern day Arabian horse.

4 Million years of Modern Horses



Hippidion

Approximately 3 million years ago the Great American Biotic Interchange occurred when the isthmus of Panama connected North America and South America (Franzen, p.143). *Hippidion* was an equine found in South America and a descendant of the early genus *Equus*. The earliest horse fossils found in South America are close to 2.5 million years old. Along with *Hippidion*, a group of fossils known as “New World Stilt-Legged” (NWSL) horses have been determined to descend from *Equus*, and not an out-group as previously thought (Wienstock, 2005). *Hippidion* was one-hoofed and adapted to mountainous terrain, amazingly surviving until just after the last ice age. It was pony-sized, and characterized with extremely deep and delicate nasal bones (Franzen, p.143-144).

Genus *Equus* emerged from *Dinohippus* nearly four million years ago in North America and diversified into many extinct and extant (living) species that we know today. They spread over the

CABALLINE



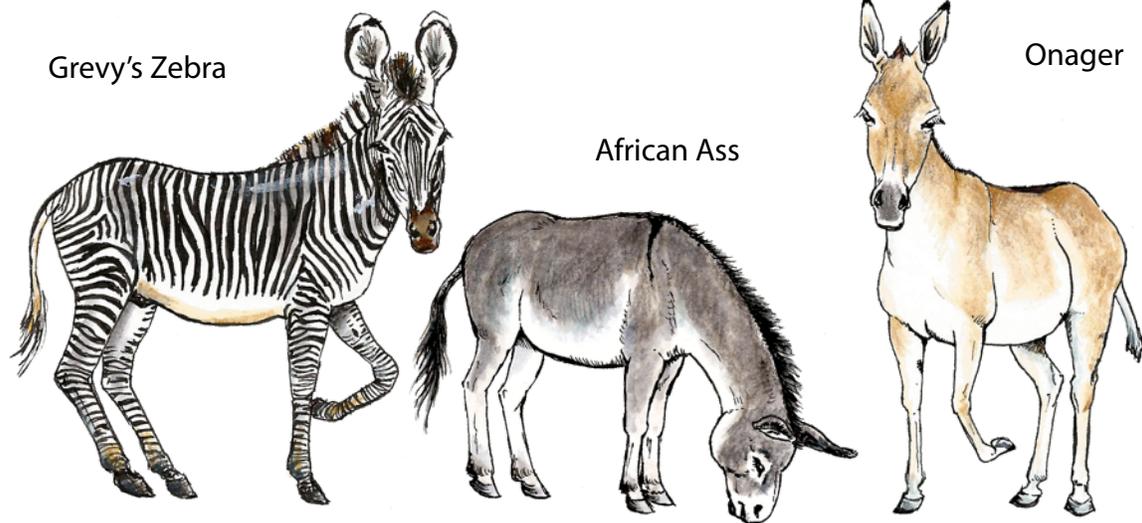
Przewalski's Horse



Domestic Horse

Bering Strait land bridge into Asia, reaching Europe and Africa. *Equus* diverged into two main groups about 2-4 million years ago: Caballine and Non-Caballine. Caballine refers to true horses: *E. ferus caballus* (domesticated) and *E. ferus przewalskii*, the wild Przewalski's horse (critically endangered) and the extinct Tarpan. Non-Caballine horses include all zebras, asses, and onagers. Ironically, *Equus* species thrived in the Americas, but became extinct about 10,000 years ago at the end of the last ice age. Along with many other prehistoric species in the Americas in a "megafauna" extinction event as a result of late Pleistocene climate change (Kefena, 2012). Over-hunting by early humans may have contributed in these extinctions (Azzaroli, 1992).

NON-CABALLINE



The domestication of horses is still hotly debated as to when and where it occurred, but is believed to be 6,000 years ago in the steppes of Eurasia (Kavar, 2008). New genetic studies indicate that the domesticated horse came from a limited number of stallion ancestors and a large number of mare ancestors and from multiple geographic locations spread throughout Eurasia (Kefena, 2012). As research continues, and fossils are uncovered, we will expand our knowledge of these amazing and beautiful animals that bring diversity to our ecosystem, and companions to our lives. Conservation efforts continue to try and preserve the wild survivors of this family. In one case, to even bring back some of the beauty that was lost with *The Quagga Project*, using selective breeding.



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