Chapter I-1

The 57 Million Year Old Pedigree

The evolution of the horse is a subject that has often been written about since it became the classic example of the theory of evolution brought to public light by Charles Darwin and Alfred Russel Wallace. No doubt, part of the reason it has been so popular among evolutionists can be accounted for by the sheer numbers of bones and teeth that have been discovered over time. Few other animals have left such a clear trail of evolutionary development for modern man. Blah…blah….blah.

In such a manner so many books start their vague reviews of equine evolution. Introductions to this topic have often proven confusing bits and pieces of equine ancestors, over an unimaginable number of years, in which there is an unclear description of their distribution over the planet. During these periods of time, rarely do they inform the role of climate, environmental conditions or the influence of inter-continental or inter-hemispheric connections. I have never doubted that these authors had the capacity to do more. Instead, I have concluded that they considered the evolution of the horse an uninteresting topic to readers and thus it was only lightly touched upon. After all, what does the information about three- and four-toed little animals have to do with the modern domestic horse that has captured our fascination for equitational disciplines, conformational and performance competitions, and modern breeding programs? A LOT!!

If we take the time to read a more detailed account of the various genera that contributed to the eventual existence of the horse (family: *Equidae*, order: *Perissodactyla*, genus: *Equus* and species: *caballus*) we could obtain a much greater understanding about the reasons behind their anatomy, their instincts and their capacity to learn the desired behavior we wish to impart upon them. Investing some time mulling over a description of animals that have hard-to-remember Latin names could result in figuring out a great deal about modern equine behavior. For example, we can help establish why horses groom each other, why horses establish a pecking order, why horses are attentive of objects so far away from them, why horses have splint bones or chestnuts or ergots -- or maybe even realizing that all these actually exist -- why horses are able to sleep standing up, what enables horses to run fast for such long distances, why horses are able to thrive in areas unable to maintain cattle and host of additional interesting information that is embedded in the genes they have inherited over millions of years from a variety of remarkable relatives.

Defining Geological Time

Before delving into this topic, I find it necessary to review some of the terms used to distinguish the divisions of time in the Earth's history. In my own readings I have frequently found it confusing that the words "Era", "Period" and "Epoch" seem to be used to describe different things by different authors. The clearest understanding of these concepts I have come across is in the book Principles of Physical Geology by Arthur Holmes. In this old text, the classifications of world time were compared to the parts of a book. As a result, the broadest classification that would compare to the volume of a book is referred to as an "Era". The chapters of the book would correspond to the "Period". The sections of a chapter would in turn be referred to as the "Epoch". The paragraphs would relate to the "Age" and of course the words themselves would correspond to the specific years.

Table I.1
The manner in which geological time in world history has been broken down:

Era	Periods	Epoch	Age	How many years ago it lasted (related to 2,000 A.D)
Cenozoic Era (meaning recent life)				70 million years ago until the present
	Quaternary Period			1.75 million years ago until the present
		Holocene		10,000 years ago until the present
			Iron Age	3,000-2,500 years ago
			Bronze Age	5,000-3,000 years ago (in Iberian Peninsula)
			Copper Age	8,000-5,000 years ago ??
		Pleistocene		between 1.75 million and 10,000 years ago
			Stone Age ?	
	Tertiary Period			between 65.0 and 1.75 million years ago
		Pliocene		between 5.30 and 1.75 million years ago
		Miocene		between 24.0 and 5.30 million years ago
		Oligocene		between 34.0 and 24.0 million years ago
		Eocene		between 54.0 and 34.0 million years ago
		Paleocene		between 65.0 and 54.0 million years ago
Mesozoic Era (meaning intermediate life)				between 190 and 65 million years ago
	Cretassic Period			between 120 and 70 million years ago
	Jurassic Period			between 150 and 120 million years ago
	Triassic Period			between 190 and 150 million years ago
Paleozoic Era (meaning ancient life)				between 500 and 190 million years ago
	Permic Period			between 220 and 190 million years ago
	Carboniferous Period			between 280 and 220 million years ago
	Devonic Period			between 320 and 280 million years ago
	Siluric Period			between 350 and 320 million years ago
	Ordovicic Period			between 400 and 350 million years ago
	Cambric Period			between 500 and 400 million years ago
Proterozoic Era				
Archeozoic Era				
Eozoic Era				
Non-Documented Era				
Origins of the Earth				around 2,000,000,000 years ago.

Note:

1- Primary Period was classified by crystalline earth strata, the Secondary Periods by compacted strata, and the Tertiary Period by loose strata. The Quaternary Period that followed was just an extension of the nomenclature that had been established by geological characteristics of earth strata.
2- The Ages are not determined by geological parameters, but instead by the point in time when the use of these metals was incorporated into various societies. The years listed refer to these Ages in regard to the Iberian Peninsula.

Importance of the Tertiary and Quaternary Periods

Insofar as the interests of this book are concerned, we will concentrate on the more recent Cenozoic Era that covers the Tertiary and Quaternary Periods. The Tertiary Period distinguishes itself as the time in the Earth's history when great numbers of mammals started to fill in the gap left by the disappearance of the great reptiles that dominated the Earth in the Mesozoic era. It is known that mammals existed as early as the Jurassic Period, but they were comparatively weak specimens next to the reptiles that efficiently occupied the sea, land and air of this period.

The Quaternary Period is most often characterized by the appearance of man. There is no doubt that man has played a key role in both the propagation and disappearance of a variety of equids throughout their evolutionary path. It is known that the initial interest of man was in hunting the equids for food. Interesting relationships and/or coincidences can be contemplated between the appearance of man and corresponding changes in the populations of equids throughout the world. Man has been responsible for domestication of various species of the Equus genus and this bond is part of the ongoing story that began in the Quaternary Period.

Equally as important to our topic is the fact that during this period there was a significant cooling of the planet, the likes of which had not occurred since the glacial times of the Cambric and Permic Periods. The importance of climate can be evidenced by the fact that the Quaternary Period is also divided into the periglacial, glacial and postglacial periods. All of the Quaternary Period can be classified into one of these three categories. In fact, it can be argued that even in the present we may be at the start of another interglacial period.

The consequences these expanding ice sheets had on the development of the horse are multi-factorial. The four glacial advances of the Quaternary Period, known in Europe* as the Giuntz, Mindel, Riss and Wiurm and in North America as Nebraskan, Kansan, Illinoian and Wisconsin, all invaded, to some degree, lands that were sites and potential sites of habitation for the various ancestors of the horse. As significant as the cold temperatures of the glacial periods were in affecting Quaternarian flora and fauna, the interglacial periods were probably just as important since they covered a greater number of total years. Some of these interglacial periods maintained cool temperatures for as long as 300,000 years. Others, during proportionally shorter periods, created drastic environmental changes in as much as 75,000 years of acute global warming.

It is important to realize that throughout all these incredibly diverse conditions, the story of the evolution of the horse took place. At times these hippomorphs seemed incredibly adept and thrived with vigor. Just when millions of years of perfect adaptation instilled a profound sense of security, they unexpectedly had to encounter a changing world, which forced them to adjust. This led to many varieties of equids, the majority of which reached generational dead-ends. Time and again the world challenged their existence and, invariably, some representative surged ahead to new epochs in time. Abrupt changes in climate, topography, nutrient resources and efficacy of a variety of predators in their habitat were unable to stop the evolution of equid specimens. Although many related families died out, a good number managed to survive.

Suddenly, for reasons no one has been able to explain, the equids, along with many other mammals of the Quaternary Period, were faced with the seemingly inevitable prospect of extinction. How much of a role man played in the time it took to reach this crossroads is only speculation. However, we DO know for certain that it was man's intention, and the horse's disposition, that whisked the horse away from this dreaded kismet. The ultimate salvation came about in the form of one the most intense domesticated relationships. Perhaps this was the greatest equine adaptation of all. Had they not submitted to a useful relationship with man, we would most likely be mentioning the horse alongside the mammoths, the giant sloths, the hairy rhinoceros and saber-toothed tigers.

If we are to understand the horses of any breed, in any region of the world, it is important that we appreciate the impact of the interesting history that precedes every equine individual we are lucky enough to have contact with today. It is impossible to have a true grasp of this without simultaneously comprehending the environment that surrounded the equines in their respective epochs of existence.

Hyracotherium

Depending on the references that one consults, the evolutionary premise of the Yale paleontologist O.C. Marsh is summarized in an account that starts back 50 to 60 million years ago with the oldest equid, termed "Eohippus" in 1873 by E.D. Cope. The "Eohippus" (which means dawn horse), was found to be identical to the European animal Sir Richard Owen studied in 1839 and named *Hyracotherium.* Due to the fact that in science the oldest name takes precedence, this Eocene equid should be more correctly referred to as the *Hyracotherium.*
* Specifically the Alps as three parts of Europe had different names for the glacial events.

The *Hyracotherium* was a small mammal that lived in the underbrush of the forests and swamplands, where it foraged on the leaves, tender shoots and fruits of trees and forbs, which had higher nutritional value than grasses. The humid, tropical climate that surrounded the *Hyracotherium,* in what are now the North American states of New Mexico and Wyoming, made for specific physiological requirements that assured its survival. Body size and probable heart rates would indicate they probably were not very long-lived, only living an average of about four years
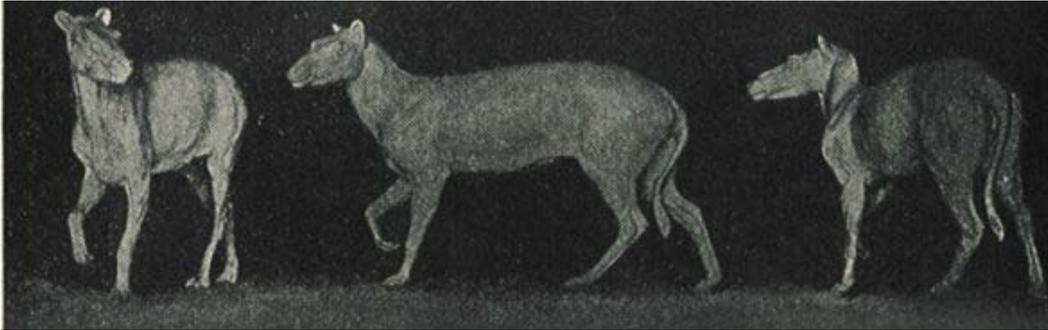
Figure I.3 Ch. R. Knight reconstructed the *Hyracotherium's* body based on fossil skeletons

The narrow-bodied *Hyracotherium* was 25-40cm in height (10-16"). Various authors have compared its size to that of a large house cat (10-12" and 20 lbs), a poodle (10-15" and 15-25 lbs.) and a fox terrier (15" and 18 lbs). This would make one think the *Hyracotherium* must have weighed between 7 and 12 kg (15 and 26 lbs).

The *Hyracotherium* featured long hind legs that supported a well-muscled hindquarter that was distinctly taller than the flat withers. Their ulna and radius bones were separated, permitting limb rotation. Their necks were short and tubular, and their heads were short muzzled with a sheep-like appearance. Their jaws were narrow and due to the more compressed articulation it could only be moved up and down and sideways when used for chewing (the modern horse still has a very limited forward and backward movement of the jaw). In spite of their long slender tail with a distal (at the end of the appendage) tuft of hair and short ears, the overall physical appearance was similar to a giant hare. This fact was responsible for having been assigned the name of *Hyracotherium,* which means "rabbit-like animal".

Figure I.4 Heinrich Harder painted his interpretation of what the live *Hyracotherium* would look like.

Due to hind legs that were 40 percent longer than the forelegs, it's thought that the *Hyracotherium* probably had a semi-hopping gait when moving carefully about the forest floors. It is estimated that they should have been able to run at a maximum speed of 54 km/hr. However, their scansorial body form (this is a shape that is adapted to the life in the thick underbrush in humid climates with dense vegetative cover) meant they probably had a fast acceleration that led to a burst of speed of short duration combined with a capacity to dodge and zigzag laterally to evade predators until they could run under brush for cover. Unlike predators that depend mostly on a rotary gallop, the *Hyracotherium* had a preference for a transverse gallop (same lead in fore and hind legs) that is still the predilection of the modern horse. This has been, in part, a result of the fewer and smaller-sized lumbar vertebrae in the equids. The fact that they are highly articulated also limited the rotation of the pelvis on the loin.

The contemporary animal that appears most like the *Hyracotherium* would be the *Agouti paca Linnaeus* that is commonly known as "Tepezcuintle" or "Conejo Pintado" (spotted rabbit). This giant rodent with a very similar scansorial body form inhabits tropical forests and jungles from Mexico to Paraguay. They differ from *Hyracotherium* in the anatomy of their teeth and tail, but the likeness of their overall conformation and size is uncanny. The *Agouti paca* is between 27 and 31 cm (10.6-12.2 inches) in height and weighs between 5 to 12 kg (11-26 lbs.) Like the *Hyracotherium,* the *Agouti paca* has four toes on the forelegs and three functional toes on the hind legs with two small vestiges of the first and fifth digits present. Additionally, like the *Agouti paca*, the *Hyracotherium* is thought to have had the hair coat color and pattern of the fawns of modern white-tailed deer that blended in well with their surroundings. This resulted in a natural camouflage that facilitated hiding as the main defense against predators.
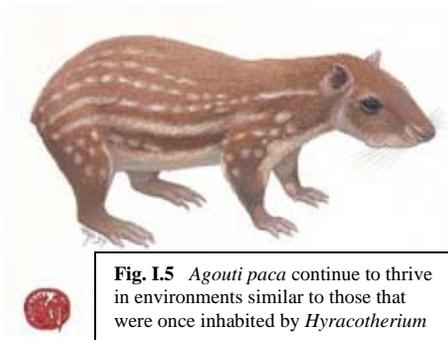

Fig. I.5 *Agouti paca* continue to thrive in environments similar to those that were once inhabited by *Hyracotherium*

The four toes the *Hyracotherium* had on the forelegs and the three toes they had on the hind legs were meant to give more traction for maneuvering and fleeing from dangers in the soft terrain they inhabited. This odd combination of appendages can still be seen today in the tapir, a distant relative that still inhabits damp forest settings between Mexico and northern Argentina and southern Brazil.

The tapir´s toes have large, tough nails much like the feet of another descendant of the *Hyracotherium*, the rhinoceros. This seems reasonable when we realize that the *Hyracotherium* also had thick digital toe pads, distal metacarpal and metatarsal pads and proximal metacarpal and metatarsal pads on each of its 14 toes, with thick cuticles or "hooflets" that looked like minute hooves, on each toe.

The teeth of the Hyracotherium were composed of three sets of molars, four sets of premolars that were distinctly smaller, a set of canines and three sets of incisors. The canines were large and probably important in fighting for and maintaining a desired mate. Since males had larger and more defined canines, they were also probably used in establishing sexual dominance. The teeth were not as hard as those of modern day equids, and possessed molars with a coned-shaped cusp that was slightly connected in low crests that were perfectly adapted to the soft nature of the leafy and fruit diet.

It is known that this key ancestor of the horse had a proportionally larger brain than other herbivores of the time. As it evolved, the cerebral capacity had always been at the forefront of its fellow herbivores. To this day the horse's superior development of the cerebral neo-cortex is attributed to a greater capacity for learning from associating various sensory stimuli. In his book, *The Nature of Horses*, Stephen Budiansky theorizes that originally the larger brain of the *Hyracotherium* and its descendant may have been essential for the selective skills of browsers and grazers. No doubt, in making the transition to plains dwellers that were more viable prey for predators, the aptitudes related to a greater intellect were also critical for its survival.

Although the Hyracotherium came into existence in the Eocene epoch, for around 30 million years they stayed pretty much the same. This prolific mammal increased in numbers rapidly and was forced to move to new territories to sustain ever-increasing numbers. In the

early Eocene it migrated across the Greenland "bridge" to the British Isles and the rest of Europe. There it gave rise to various European genera of equids, such as the Paleotherium, all of which died out by the middle and late Oligocene. With time, it spread throughout North America and across various land barriers to Asia, Eurasia, Europe and back. South America, on the other hand, would still not have the presence of an equid for some time.

Such a long period of efficient suitability genetically ingrained many traits in future generations that would have to adjust to varying conditions. The *Hyracotherium* was a highly territorial animal that was mostly monogamous with close social bonds between mates. The mutual grooming that is commonly seen in equines today may very well be a vestige from the need of early equids to have these close paired relationships.

As a forest inhabitant, the *Hyracotherium* probably had a more intricate repertoire of communicative vocal sounds. The whinny and squeal of the modern equine are still vocal expressions that carry over long distances and are used in a wider array of social interactions than is common in most other wild herbivores. It is most likely that *Hyracotherium's* dependency on territorial definition was responsible for the fecal markers (manure piles) that are commonly placed by stallions today. Many of these examples are cases in point that as animals evolve, some traits that

Fig. 1.6 Mutual grooming is a behavior that traces back to the origins of the equids.

were not crucial to select against, in fact get carried over into new environments that no longer rely on their existence.

Orohippus and Epihippus

Two million years after the appearance of the first equid, the *Hyracotherium vassacciense* gave rise to the *Orohippus.* Although not as widespread as the Hyracotherium, this genus coexisted with its direct ancestor during the early Eocene Epoch. The name means "mountain horse" because Professor O.C. Marsh found the first fossils in an isolated mountain of Wyoming in North America. In fact, the *Orohippus* didn't typically inhabit mountainous terrain. Later, more fossils were found in the state of Oregon and such findings show a span of at least seven million years for this genus. Physically, the *Orohippus* was very similar to the *Hyracotherium,* and the main difference was more enlarged middle digits on all four feet and a loss of the vestiges of the first and fifth digits in the hind legs. The last premolar also took on a shape of a true molar and thus offered the Orohippus a greater grinding surface for eating tough vegetative matter.

Forty seven million years ago the *Epihippus* evolved and was almost identical to the *Orohippus,* except for the fact that another premolar had changed to look like a true molar, thus providing five sets of grinding teeth capable of utilizing a coarser diet.

Mesohippus

The "middle horse" or Mesohippus appeared about 37 million years ago, during the late Eocene Epoch. However, the genus is more associated with fossil sites in Colorado, Nebraska, North and South Dakota and Canada, which have confirmed its existence as late as 32 million years ago, during the Oligocene Epoch.

This was a larger animal that started evidencing important changes that looked more horse-like. Its 61 cm (24 inches) were achieved through a proportional elongation of all the bones of the leg. Along with the lengthening of the leg bones, there was also an augmentation of the neck as well as the face and nose of the head. Likewise, the brain is much more horse-like and offers the still scansorial body form more recourse to outwit its predators. The shallow fossae (a hollow or depressed area in the anatomy) below the eyes of the *Mesohippus* would be another characteristic that is solidly identified with the evolution of equids. Moreover, it's not until the arrival of the genus *Equus* that it disappears from equid anatomy.

The *Mesohippus* genus is also the first to lose the fourth digit of the forelegs, establishing the most representative characteristic for equids over time, that of being a three-toed animal. Since all three toes were weight-bearing, the pads of the foot still had an important function.

The *Mesohippus* also changed another small triangular premolar to the squared "molariform" that is more proficient at grinding. With six sets of molar and molar-like teeth, the *Mesohippus* was more suited to incorporate some bark and grass into its diet. However, the low crowns and soft composition didn't permit it to depend solely on coarse grasses.

Although originally this genus was traditionally thought to be in the direct evolutionary chain that led to the *Equus*, palaeontological findings are now suggesting that this descendent of the *Epihippus* may have been a parallel branch to the *Miohippus* which actually existed in the same time period as the closely related genus that went on to play a more decisive role of the *Equus* family tree.

Fig. I.7 Heinrich Harder's illustration of a herd of *Mesohippus* venturing out into the grassy plains.

Miohippus

In about five million years the *Mesohippus* went through an anagenic transformation into the slightly taller *Miohippus*. This means that the ancestor slowly changed into another genus and thus disappeared as the changes took place. This differs from the cladogenic transformation that we saw with the *Hyracotherium* that gave rise to the *Orohippus,* but the two equids in fact coexisted side by side for a good many years before the more adapted genus prevailed.

Most of the fossils of the *Miohippus* are also found throughout the western United States, but there have also been some discovered in the southeastern part of the country. Dating this material gave rise to the discovery that the *Miohippus* lived from 32 to 25 million years ago. The name would imply a relationship with the Miocene Epoch, and in fact, Professor Marsh thought he had found this genus in Miocene rocks. Unfortunately, science has to live with this misnomer because the *Miohippus* is solidly related to the Oligocene Epoch.

The Miohippus was the size of a pony, weighing between 100-175 kg (220-385 pounds). Their third metacarpal and metatarsal bones, as well as the first, second and third phalanx of the corresponding digit became thicker and more prominent, supporting a major portion of the body weight. The forelegs and hind legs were more similar in length, providing a less convex dorsal profile than the *Hyracotherium,* but still maintaining a degree of the high-rump posture. All these structural changes were more fitting for the ability to run smoothly over a longer distance, as opposed to hopping over obstacles or only sprinting short distances.

The facial portion of the Miohippus skulls were elongated, creating a space between the premolars and incisors that in the distant future, would play an important role in bit placement for domesticating the modern horse. The bars of the mouth of the modern horse are available for equitational purposes because of the need to elongate the jaw so that the frontal incisors could reach short growing forage that then the tongue passes back to the grinding mechanisms of the molars before swallowing.

The Miohippus' facial fossae were more pronounced. Their teeth still had a low crown and a consistency that was still only suitable for browsing leaves, shoots, tender bark and tubers. However, their brains became more complex and served them well as they started to wander into open areas away from the security of the forest.

Several species of *Miohippus* have been discovered in the fossil records of North America. The *Miohippus celer* species appeared first, followed by the *M. westoni* and the *W. assiniboiensis*. Actually the *Miohippus* marks an important change in the equine evolution, as from this genus as many as a dozen other genera appeared in the subsequent Miocene Epoch. These descendants have been classified into three distinct groups: the three-toed browser, the pigmy browser and the grazer.

In the middle of the Oligocene, the interhemispheric connections were split, so the *Mesohippus* and *Miohippus* could only exist where they came into existence, in North America. It is interesting that one group of descendants should be three-toed browsers that spread into Eurasia in the later part of the epoch when the Bering land route was exposed once again. This includes the genus of *Anchitherium* that in turn led to the genera *Hipohippus* and *Megahippus*, all of which were extremely successful in the Old World. They later diversified into other genera and many species, some of which were probably the first equids to enter Africa.
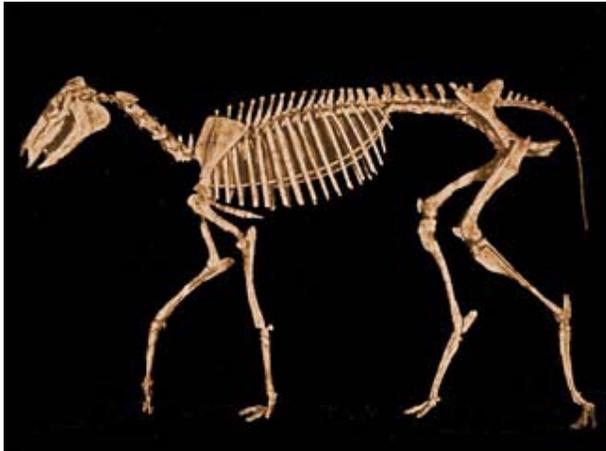

Figure I.8
The *Miohippus* developed longer legs and a less convex dorsal profile giving it the ability to run more efficiently over long distances.

The second offshoot of the *Miohippus* was the minute horses that were represented by the *Archeohippus* and *Kalobahippus*. Some of these equids were smaller than the original *Hyracotherium* and thus are an important example that the genetic variation in evolution has no particular direction. It is easy to follow the evolutionary path of the equine and assume that this was one of ever-increasing size. Interestingly, the *Miohippus* gave rise to both the larger *Hipohippus* and the pigmy equids from this group, providing evidence that when genes are combined by chance, all alternatives are possible. The contribution the *Miohippus* made with these two branches alone was significant in the variety of equids it placed in the world. However, the change from the Oligocene to the Miocene Epochs marks a climatic change in the world that ended the tropical environment composed of continuous forest and gave rise to open areas with large grasslands. The camels were the first ruminants to evolve in North America and they were already making efficient use of the fibrous source of nutrients in the savannahs.

The opportunity for the *Miohippus* to do the same led to the formation of the third group of descendants that developed some key transformations for the evolution of the horse. It would be the grazing equids that would find a niche that assured their projection into the future.

Since this was the only branch that reached the present, it is a classic example of how nature provides multiple variations in an effort that one of the genetic makeups will be successful in a changing environment. Many of these variations are successful in terms of surviving in the present, but only the variety of genotypes gives hope that some will be suited to unpredictable changes that come forth in the future. Those that are so suited will push the evolutionary trail past another crossroads.

Parahippus

Around 20 million years ago, a crucial stage in the evolution of the horse took place. The geological formation of the North American Rocky Mountains caused a climatological change in the flat stretches of land to the east. The forests were substituted with plains that provided a significant difference in the food supply. The increased proportion of drier savannahs, with coarser sandy soils and thick, deep-rooted grasses was a significant factor in creating a multitude of genetic transitions that followed.

In this Miocene Epoch, 24 million years ago, the *Parahippus* appeared. Slightly taller and leggier than the *Miohippus*, like most grazers in the Equidae family they would be refined, gracefully moving creatures.

The two atrophied lateral digits no longer touched the ground and the lateral digital toe pads started to atrophy from disuse. This left all the weight to be carried on the hoofed middle toe, which started to take on a more erect position from the development of ligaments that attached to the toe, providing a springy suspension mechanism.

Sideways displacement was becoming much less important. This was the first equid to no longer escape predators by the means of the scansorial method of fleeting accelerations and erratic lateral trajectories through thick vegetation. The focus now became early detection and enduring speed over straight-line trajectories.

Most predators could only accelerate for a matter or seconds using limiting phosphocreatine (the most important source of high energy for muscle contraction) pathways as an anaerobic source of energy for their predominantly fast twitch muscles. Along with the audacity that took the *Parahippus* into the open plains came the development of an anaerobic glycolysis (breaking down nutrients to sugars and simpler substances that are readily used by the body without the need of oxygen) mechanism that provided them real speed for closer to a minute. Still, their best recourse was preventing predators from getting within attack range and thus resistance, more than speed, became their saving grace. For this, equid muscles developed high proportion slow twitch and high-oxidative fast twitch muscles that could respond to the challenge. The result of this hardware was an efficient oxygen-burning pathway that could provide intermittent, or partial, aerobic efforts that could maintain respectable speed over long distances.

Important changes were noticed in the teeth, as this was the first equid with slightly higher crowns and a hard cement-like covering that permitted more dental longevity when utilizing prairie forages in its diet. The *Parahippus* had ridges on its molars similar to those of modern horses, suitable for shearing hard tufts of grass. By 17 million years ago, the *Parahippus leonensis* was so similar to the Merychippus that a very smooth anagenic transformation is exemplified.

In reality these resemblances have been most significant in how the *Parahippus* genus has been included in the traditional palaeontological literature. New findings indicate that a crucial crossroad in equid evolution may have taken place in the different types of *Parahippus* descendents which Richard C. Hulbert informs us, in his chapter in *Horses Through Time*, have been classified as Hipparionni and Equini tribes. It seems that what previously had all been lumped up in the *Merychippus* genus were in fact specimens of various other genera that evolved from the *Parahippus*.
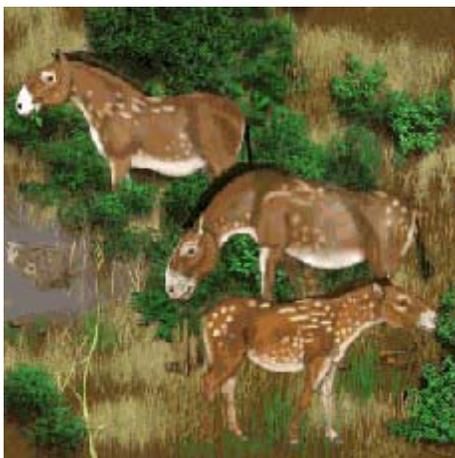

Fig. I. 9 The *Hippidion* was the most prevalent equid in South America. This illustration was based on fossils found in Tarija, Bolivia.

The *Cromohipparion*, *Nannipus*, *Hipparion*, *Neohipparion* and *Pseudohipparion* are some of the genera in the Hipparionni tribe. This tribe composed of smaller and more slender equids dominated North America between 14 to 3 million years ago. Honduras was as far south as they reached as none of them ever entered the South American continent. By 11 millions years B.P. the Hipparion had crossed into Asia and Europe and well down to into Africa before going extinct about 2 million years ago.

Of course the Equini tribe is the one that most interest us as this branch of the *Parahippus* was responsible for the *Pliohippus* and *Astrohippus*. The latter was not only accountable for the *Hippidion* and *Onohippidium* that thrived in South America, but also is the direct ancestor to the *Dinohippus* that gave rise to the *Equus* which spread throughout the entire world with vigor.

Although it never strayed far from the edges of the forest, the *Parahippus* took a bold step to venture out in the open. This increased substantially their potential habitats in a temperate climate world that was increasingly less forested. The fast predators of the day would assure selection pressure that would improve the adaptability of the equids to the grasslands even more.

Merychippus

In approximately another five million years, the *Merychippus* evolved in the same Miocene Epoch. This was the tallest equid to evolve thus far, reaching a size of approximately 1.07m (42 inches) while weighing around 190 kg (418 lbs.). It was widespread around America, Eurasia and Africa, evidencing the existence of landmasses that connected the continents once again.

This was a decisive stage in the evolution of the horse, as there was a permanent transition from being a browsing animal to a grazing one. The change in diet was also a change in habitat, as the grasses grew in the open spaces where there was greater vulnerability to predators. As a result, this prey animal could no longer confide in its ability to hide and go unnoticed. Now it had to detect its enemies with sufficient time and flee fast enough to avoid being captured.

As a result, the *Merychippus* had a longer and wider jaw that provided stronger muscles for grinding the hard phytolithic forage. The longer jaw also had the convenience of distancing the laterally placed eyes from the ground. This offered the possibility of greater peripheral vigilance of predators while grazing. It also provided the needed space for the longer roots of the rows of larger grinding teeth.

The premolars evolved to look more like molars, thus increasing the area of grinding capacity. The teeth developed a much taller crown (a characteristic referred to as "hypsodonty") with multiple folds of enamel that were further reinforced by an overlying layer of a very hard cementum, to withstand the wear and tear of grinding the tough prairie or savannah grasses. These crowns were made up of substances of varying hardness that created sharp edges as they were worn at different rates. These resulting pointed rims were useful for cutting the long fibrous forage they pulled into their mouths with their strong, dexterous lips. Eventually, the equid developed "hypselodontic" teeth, which means that they never stopped growing. In this manner, their teeth would not become a limiting factor when confronted by the eroding properties of grazing soil-contaminated, silicanous grasses. Of course today these traits, which are still part of the modern horse, create the need to continually float (rasp with a dental file) teeth with long sharp edges that cut into the sides of the mouth.

The importance of vision to a prey animal is obvious, and the equines would eventually develop the largest eyes of all land mammals. Not only did their eye size and placement offer them a potential for a 357° field of sight, but the lens shape, as well as the location of concentrated receptive ganglia on the retina, offered an ideal focus for long distances. Without the dense forest foliage to give them nocturnal security, the eye also developed both a concentration of light sensitive rods and a light-reflecting tapetum (an iridescent layer of cells that give the eyes the property of shining in the dark) behind the retina, permitting acute night vision. Additionally, the equines have been found to have a dichromatic vision with rods that can detect only red and blue colors.

Fig. I.10
The horse developed the largest eyes of any land mammal.

This peculiar kind of color blindness makes the colors of the spectrum for which they don't have cones (yellow) and colors that require stimulating both blue and red cones equally (such as green), appear to be in black and white. In an environment that is a sea of green and yellowish grasses, no doubt this type of vision would help pick out any animal or object that does not blend in well with the surrounding colors.

Stephen Budiansky interestingly points out that as the equids evolved from browsers of nutritious leaves and shoots to grazers of grasses of marginal nutritional value, they found a competitive edge with ruminants of similar size that were unable to maintain themselves on such low-quality diets. Although the equids were monogastric (single-stomach) animals, they did have a functioning caecum (a large fermentation vat that anatomically is a much-enlarged version of our appendix) that was capable of digesting the cellulose in high-fiber diets. It is

known that the singular make-up and anatomical position (posterior to the stomach and small intestines) of the caecum, leads to a lower digestibility of feedstuffs than the four compartments that precede important sites of absorption found in ruminants.

The advantage of the equids was to be found in the fact that they were not as limited in the amount of ingesta they could push through their digestive tract. By not having to stop to ruminate and chew their cud, they were able to graze continuously. Furthermore, the rate of passage of ingesta in ruminants is slowed down even more when consuming poor-quality feedstuffs.
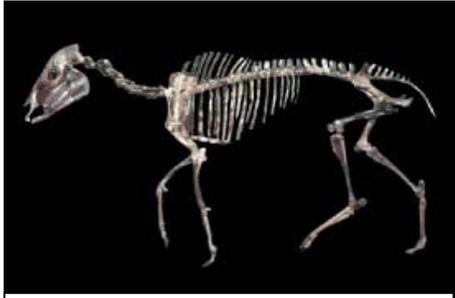

Fig. I.11 The *Merychippus* had a more horizontal dorsal line as well as longer and wider jaws that permitted grazing tough grasses while maintaining visibility of the surrounding areas.

The equid, on the other hand, met this type of nutritional limitation by eating more and thus offset their lower digestive coefficients by consuming a greater number of net calories in a day. As a result, the equid has had a greater range of possibilities in choosing the areas it wished to inhabit, oftentimes surviving in areas where there was little competition from other herbivores.

The change in diet during the middle of the Miocene Epoch also brought about an important change in the social structure of the equids. In *The Nature of Horses*, the author points out that small animals inhabiting areas that are abundant in rich feedstuffs have a tendency towards monogamous social patterns. As females become less concentrated, a male may tend to two mates. The territories of the females are defined, marked and defended aggressively by the males that show a distinct difference in conformation, as well as greater body size, that is referred to as *sexual dimorphism*.

The *Hyracotherium* fit this pattern well, as it has been determined that male-to-female ratios were between 1:1.5 and 1:2, while males showed substantially larger canine teeth and skull size. However, in the Miocene Epoch, when the equids changed from the forest habitat to the grasslands and their selected diet required roaming around larger areas, the social structure changes to a polygamous one. In order to preserve the proliferation of the genus, in this epoch it became important that a male tend to a small harem of females. Since the nutritional resources were no longer provided by a restricted area, the reproductive functions also had to divorce themselves from a specific locale. By moving over vast expanses as a group, sexual functions moved with them.

Life in a herd brought about various adjustments as well. The physiological improvement in prey animals is usually a cause for upgrading the qualifications of predators. So, as the camels in the open plains created a need for a faster, more intelligent predator, efficient feline and canine-like species developed to the point where they were able to effectively hunt them. The saber-toothed tigers provide a classic example. These more effective predators brought on a need for the grazing equids to rely on each other for the early detection of stalking predators hidden in the brush.

In open terrain, animals that were already fine-tuned to spotting potential dangers found visual communication amongst its group more convenient than vocal interactions. Certain functions, such as spotting danger, were no longer an egotistical trepidation. No doubt, a multiple set of eyes would see more than any single individual was capable of. Yet, when taking flight on the spur of the moment, it was crucial that each member of the herd know exactly what was expected of them. The oldest and more experienced took leadership positions over familiar routes. The young and submissive mirrored the movements of their dominant counterparts, and the strongest either herded those that lagged behind, or boldly took the forefront to confront potential threats to the group. Decisions and concerns could be reserved for crucial events, if each individual could be expected to accept its position in the herd.

The hierarchy that established a pecking order vitally arranged the group members. This was not only helpful when mobilizing the group, but also when traversing constricted areas, approaching an unfamiliar circumstance, or taking turns to obtain vital requirements of limited

access such as water, salt, etc. By eliminating the need to compete for positions and accepting a pre-established order, the group always had the assurance that some members were on the lookout for potential danger.

What is clear is that the environmental conditions in the Miocene Epoch brought about critical changes in many of the equids and the *Merychippus* was the first that really adapted to the new surroundings. Obviously, other relatives would continue to be browsers, with softer teeth, shorter faces with smaller eyes, and still dependent on shorter legs with multiple digits. The fact that all these branches of equids eventually died out points out how vulnerable even the most adaptable of genera are. Although, many *Merychippus* where erroneously classified as such, there is still no getting around the fact that this prolific genus represented many of the anatomical changes that came about in the transition from the *Parahippus* to the Dinohippus.

Although the *Merychippus* appeared in North America about 17-18 million years ago, eventually it was widespread throughout North America, Eurasia and Africa. The *Merychippus* was responsible for the greatest ever equid population and variety. Within the genus, species such as the *M. gunteri*, *M. primus, M. intermontanus, M. slylodontus,* and *M. carrizoensis* all contributed to fossil records. By the time they disappeared 10 million years ago, they were responsible for three major groups of equids with at least 19 new species that were specialized grazers.

The "hipparions" were represented by four genus and no less than 16 species all over the world and together with the *Merychippus* and the *Nannihippus* completed the tribe we now know to be described as Hipparionini. The "protohippes" that offered yet another smaller-statured branch of equids in the *Protohippus* and *Calippus* are now grouped with the Pliohippus, Hippidion, Onohippidium and the "true equines" in the Equini tribe. Even so, no definition is 100% applicable as some undefined categories came about in the *Merychippus sejunctus* and *Merychippus isonesus* that shared a mixture of traits from parts of both groups.

Although these offshoots varied in many anatomical features, the one common denominator in all *Merychippus* descendants was the deeper and more intricate facial fossae. Perhaps the most reasonable explanation for the fossae is that this cavity was used to attach the strong muscles needed in the presence of a protruding upper lip or snout. Since the facial fossae first appeared in the *Miohippus*, and this genus is the common ancestor of all chalicomorph browsers (body forms that are adapted to semi-dense forests where leaves of forbs and/or subterranean tubers were the main diet and fleeing speed is a more significant part of the defense mechanism), it would make sense that this somehow be related to their eating habits that required a greater reach and labial (lip) manipulation.

With a long nose or more defined snout, the succulent leaves on branches of tall vegetative growth could be pulled down within reach. Likewise, such an anatomy would facilitate pulling out energy-rich roots and tubers. These functions also required the evolution of a longer and more flexible neck that is no doubt part of the common makeup in the conformation of chalicomorphs. All these characteristics can also be seen in the present day browser, the tapir, who depends on such fossae for the attachment of strong muscles that help move their snout and upper lip.

Others have speculated that these fossae enclosed scent-marking glands that help identify members of the same species. Such a mechanism exists in antelopes and other herbivores. Yet another
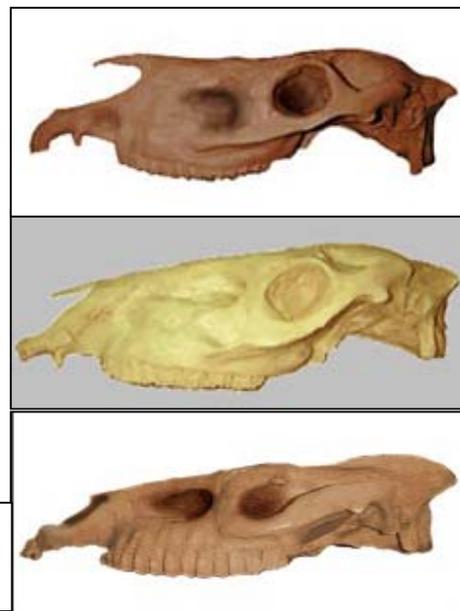
Figure I.12 – I.14   Skulls of the a) *Dinohippus* b) *Pliohippus* and c) *Megahippus* all show the facial fossae (in front of the ocular fossae) that first appeared in their ancestor the Miohippus.

hypothesis, offered in 1920, was that this space was connected to the nostrils (nasal diverticulum) and thus enabled this cavity to vocalize sounds with greater sound resonance. In light of the common parentage of the chalicomorph browsers and even the modern tapir itself, it would seem that the initial explanation for the presence of the facial fossae is more reasonable.

Pliohippus

About 15 million years ago, during the middle Miocene Epoch, another descendent of the Parahippus that became known as the *Pliohippus* coexisted and finally substituted the *Merychippus* in the mammalian fauna of the time. Most likely, the first *Pliohippus* still had three digits, but by the late Pliocene it was clearly a one-toed equid. They were taller than the *Merychippus* and were thought to bear a resemblance to some of the modern-day zebras. The main differences lied in the fact that the *Pliohippus* still had deep facial fossae and their teeth were distinctly curved.

The *Pliohippus* lived between 15 and six million years ago and fossils have been found in Colorado, Nebraska, and North and South Dakota in North America. Although the name would imply that this genus is closely related to the Pliocene Epoch, a redefinition of this epoch determined it to be a much narrower period of time than once thought. As a result, the *Pliohippus* and the many other mammals that were once thought to be from the Pliocene Epoch are now known to have been more abundant in what we now define as the Miocene Epoch.

Another factor that complicated matters is that some of the animals once thought to be *Pliohippus* have now been reclassified as another *Parahippus* offshoot that more recently have been named *Dinohippus*. This was basically due to the fact that the latter had smaller pre-orbital fossae that were intermediate between those found in the *Pliohippus* and the *Equus*, which had none.
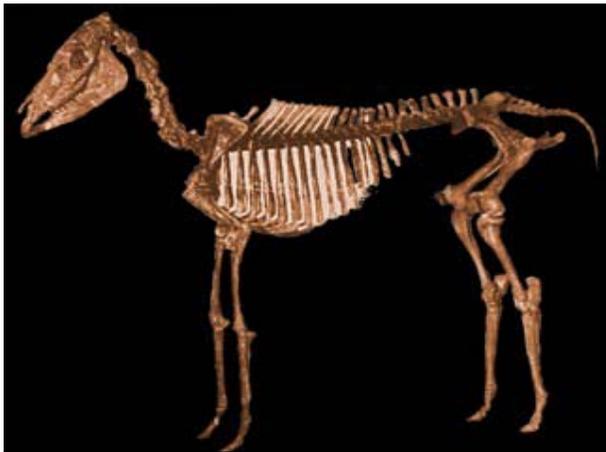

Figure I.15 Longer forearms, shorter tail, more flexible neck, more pronounced withers and a concave back, all made the true grazer known as *Pliohippus* a much more efficient running machine.

The one-toed characteristic that was becoming common in the Pliocene Epoch brought several unique locomotive qualities to the Equidae of the time. When reaching its maximum speed of 70 km/hr in unpredictable footing, the horse shows incredible stability in spite of the thin bones on unusually long legs for its body size. One of the reasons this is possible is that, in these early equid grazers, the ulna and radius of the forearm and the tibia and perone of the hind leg fused together, inhibiting the horse from being able to rotate his appendages laterally. This more limited movement offered steadier forward and backward structural conformation that assured more stability when moving at high speeds over uneven terrain.

In fact, much of the grazing equid's anatomy focused on specializing on the singular plane of forward and backward movement. In horses, the shoulder blades are positioned vertically on the body with no osseal attachment to the rest of the skeleton. Held in place by the shoulder muscles, they are free to swing back and forth and offer a greater length of stride. The equine hip does not have the typical ball and socket joint, instead it has a design of which only permits forward and backward motion. The various joints of the hind leg have grooves on the bones that prevent them from flexing sideways.

All these anatomical stabilizers reduced the amount of heavy muscle mass and bone density that would be needed if lateral flexibility were desired. By shedding all this excess weight and concentrating on the one plane of motion, the grazing equid's anatomy is better suited for long strides that can be maintained over extended periods of time.

Hyracotherium's back was originally convex. As *Miohippus* grew bigger, it also developed a longer, but still similarly proportioned back that remained distinctively high in the posterior end. On the other hand, the arrival of the *Merychippus*, the first full-fledged grazer, brought on some new body proportions. The distal appendages were telescoped out, creating a leggier animal. A greater lengthening of the fore legs evened out the forequarters with the hindquarters. A longer, more flexible neck was created by incorporating the first thoracic vertebrae into the functions of the cervical vertebrae. A more pronounced withers and a higher placement of the coccygeal vertebrae (triangular bones of the tail formed by the fusion of the last vertebrae in the spinal column); both shortened the tail and helped to dip the back.

Most of these characteristics were more exaggerated in the *Pliohippus,* which evolved to have a clearly concave back. Such a conformation offered the possibility of more efficient movement that maintained a nearly level profile when stretching out at a run. Fast felines and canines spend a lot more energy raising their back while flexing their hind legs incredibly high in order to obtain the great over reach that result in a high maximum speed. Grazing equids, on the other hand, conserved energy in the limited movement of a flatter back the motion of which alternates a semi-rigid tension and a rebound of energy when the back returns to its original form. This lower energy expenditure came from not having to raise and lower the heaviest body parts, which, in turn, permitted them to maintain relatively high speeds for a much longer period of time.

Many other herbivores have a springing ability in the limbs, but the grazing equid is unique in capitalizing the energy that is released from a semi-rigid axial (horizontally aligned) body. Although the vertical orientation of the lumbar joints promote a loin-contraction through the bending of the lumbosacral joint (union of loin and croup), the tightly interlocked nature of these vertebrae once again limit rotation and lateral flexion. Anatomically, we are reminded once again that the objective in the design of grazing equids is efficient forward and backward motion. This is accomplished by sacrificing the ability for movement in other planes.

Rather than coiling and stretching his body like a spring to obtain a longer stride, the horse achieves the desired effect by an effective suspensory system. The tendons and ligaments store energy in stretching during the weight-bearing phase, which is released when initiating the suspension phase, thus helping to project the legs forward with a much lower muscular requirement. This mechanism is particularly effective in the horse, because the single digit makes up practically one third of the length of the entire leg. Such legs, which are mostly light bone and very little muscle mass, are effortlessly put into motion by the stimuli initiated in the upper body.

The evolution of the single digit did help in obtaining a greater capacity for speed that was necessary in running away from predators. Still, some of their enemies had greater accelerations and even a capacity to run faster over short distances. The equids compensated for this by keen eyesight and a social system that always had sentinels on the look out for timely detection of potential dangers. If the equids could react well in advance to dangers, it would be their ability to maintain speed over long distances that would keep them safe from their foes. The physiological changes that permitted them to excel in endurance were equally important in meeting their needs to travel great distances in order to obtain their nutrient requirements.

As we can see, some important characteristics that later would also be associated with equines were part of the make up of the *Pliohippus* and its important to make mention of the genus where these characteristics first evolved. Although at one time this genus was considered by some to be the "grandfather" of the modern horse, more recent palaeontological conclusions classify it as a parallel rather than direct branch of the "true" horse. Still, this does not take away the relevance of the significant anatomical changes this genus exemplified in other genera that went through similar transformations while playing a more direct role in the equid evolution.

Dinohippus

Dinohippus fossils have been found from the late Miocene Epoch in North America between eight and four and a half million years ago. Not until recently was it determined that the *Dinohippus* rather than the *Pliohippus* was the direct ancestor of the horse. Moreover the constant juggling of these categories would now have us believe that the *Dinohippus* is a direct

descendent of the *Parahippus* rather than the *Pliohippus* which evolved as an independent parallel branch In fact, some species that had been previously classified as *Pliohippus leidyannus* have now been determined to be members of the *Dinohippus* genus. Perhaps part of the confusion about this genus was due to the fact that some representatives still had three toes. Still, for the most part, this was a one-toed genus that had other important traits placing it further up the evolutionary ladder.

The facial fossae of the *Dinohippus* are shallower than in the *Pliohippus,* leading scientists at one time to believe it was, in fact, an intermediate genus between the *Pliohippus* and the *Equus*, which had no preocular fossae (the anatomical depression in the skull below the eye previously discussed).

The other feature that distinguished the *Dinohippus* was the fact they had straighter teeth than the *Parahippus* and *Pliohippus*. One of the later species, the *Dinohippus mexicanus,* had the straightest teeth in the genus and very small pre-orbital fossae. Since the *Equus* has the straightest teeth of all, once again the intermediary characteristics of the *Dinohippus* seem to confirm it is a close ancestor to the *Equus*.

Another reason that the *Dinohippus* is considered the closest relative to the *Equus* is because it is the first equid to show a crude form of the "passive stay apparatus" that the *Equus* would evolve to even greater perfection. This most interesting stabilizing system that was developed by the grazing equids permitted them to effortlessly stay on their feet.   Already, previous equids had paved the way in preparation for this bit of engineering genius.

The *Parahippus* had already come up with an intertransversal joint between the sacral vertebrae (spinal bones under the croup) and the last lumbar vertebrae (spinal bones under the loin), which permitted the coiling of the loin. The dorsal spinal process of the sacrum pointed backward, towards the tail. On the other hand, the dorsal spinal process of the lumbar bones pointed towards the head. This permitted the ligaments that firmly attached to them to stretch out on the forward and backward gradients that declined from the highest point of the hip.

When the loin contracted, a space was created at the intertransversal joint (point of union of spinal processes that faced in opposite directions) that permitted the dipping of the loin. When the back was relaxed, all these ligaments were stretched tight. The structures in front and behind the intertransversal joint, in effect, hung from the apex of the hip. This was crucial in obtaining lateral balance from the other connections that tied the sacrum (vertebrae of the croup) to the lower leg.

In the *Merychippus* the coccygeal vertebrae (bones in the tail) became larger and were placed further up the back. This caused a shorter root of the tail (usually no lower than the point of the buttocks) in more advanced grazing equids, but more importantly it permitted these bones to work in conjunction with the sacral bones. The extra support became important because these vertebrae are the uppermost attachment of the hamstring muscle. With each new *Equus*-evolving genus, a longer ischium (this is a part of the pelvis that equates with the point of the buttocks, but can best be felt just inside, and part of the way up, the vulva of a mare, where the union of the right and left half of the ischium forms the floor of the vagina) also became a part of grazing equid anatomy.   Wrapping around this bone offered greater leverage on the hamstring muscles of the hind leg, as it stretched over it in route to the lower leg. This complex system of strategically located supporting muscles and ligaments served to hold up and stabilize the hind leg when a horse chose to stand in a resting position.

When the equid conscientiously desired to rest, the tendons were fixed in place on a groove upon the humerus of the forearms, and the patella was fastened into the ridge of the femur in the hind leg. In this manner, the *Dinohippus* and descendants were able to "lock" their legs in place while standing upright. This provided a unique capacity in the animal kingdom to rest at basal metabolism (a state where no effort is being made for "work" of any kind, as only the calories for maintaining body functions are required) while in a standing position. As a result, the more evolved equids could rest just as well standing, as lying down. Undoubtedly, this had its distinct advantages for a prey animal initiating a sudden departure upon detecting a predator.

Although some researches prefer to classify all the *Dinohippus* that are 7-8 million years old and younger as part of the *Equus* genus, others feel there are significant differences that

merit its classification as an independent genus. For those that prefer to think the distinction between these two genera is justified, the break off point is generally made between 4.5 to 4 million years ago when the sole survivors of the *Parahippus* descendents from the Equini tribe were all part of the *Equus* genus.
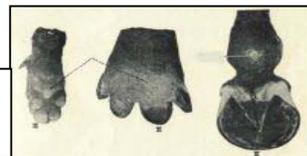
Equus

The appearance of *Equus*, the last link of this evolutionary chain, took place in the Pliocene Epoch of the Tertiary Period, four to five million years ago and around 15 million generations after the existence of the *Hyracotherium*.   There are some very distinct physiological differences that help define the *Equus*. Some of these characteristics have slowly been changing in the genera that precede the *Equus*. Then again, some of these traits are unique in the *Equus*, in spite of the fact we tend to think of them as equid traits. In reality, in many ways the *Equus* is not very representative of the many grazing equids that preceded it.

The *Equus* has:
1- **A single-toe (monodactyl)** - most other grazing equids were multiple-toed and even the more highly evolved genera had some representatives that were multiple-toed. Monodactyls still show remnants of their multiple-toed past. The second and fourth metacarpal bones (outer and inner splint bones) with little structural justification are most likely atrophied appendages. It's probable that the lost toe pads also correspond to equine anatomical features. The digital toe pads turn into the frog of the sole (this is a"V" shaped callus on the bottom of the hoof). The distal metacarpal toe pads turn into the ergots (two button-like calluses on the back of the fetlock) and the proximal metacarpal wrist pads probably become the chestnuts (callus above the knee on inner part of foreleg and below the hock on inner part of hind leg).
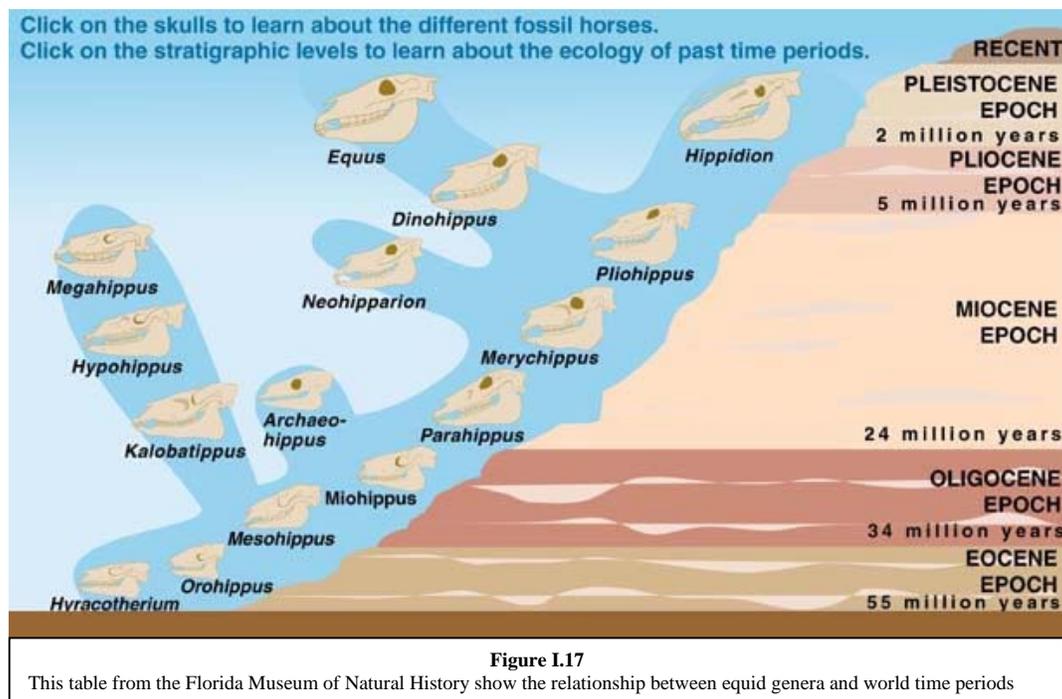

Figure I.16 Comparing a dog paw with a tapir foot and a horse hoof you can see anatomical similarities. Notice the frog on the bottom of the hoof and the ergot behind the fetlock that is pointed out by the indictor line

2- **No pre-ocular facial fossae**- all the grazing equids that preceded the *Equus* had these fossae to some degree.
3- **Very straight teeth**- the further back in the evolutionary trail, the more curved the teeth were.
4- **Large eye**- the *Equus* evolved the largest eye of all land mammals.
5- **Height**- most *Equus* that have not been manipulated by man are between 1.37m (13.2 hands) and 1.47m (14.2 hands). No wild Equidae was ever taller than 1.57m (15.2 hands),but that was a specimen of another genus that became the tallest of all equids.
6- **Weight**- having evolved during glacial and subglacial conditions, the *Equus* developed thicker body builds than previous equids. They most likely had thicker skin and hair coats, as well as a lower metabolism that promoted greater body fat reserves and longevity. Before the *Equus,* most grazing equids were light muscled, light boned and refined and stylish overall.
7- **Most pronounced withers**- the protrusion of the withers increases progressively from the Parahippus onward. This also means the *Equus* had the largest crest.
8- **A perfected passive stay apparatus**- only the *Dinohippus* had anything remotely similar.
9- **The largest equid brain-** brain size increased progressively in the genera that connected the *Hyracotherium* to the *Equus*.
10- **The equid with the most speed and stamina-** the Equus became one of the fastest land mammals based on sheer speed reached, but were unique in being able to maintain unsurpassable speed from 1-4.8 km (5/8-3 miles) and admirable speeds for longer distances of up to 160 km (100 miles).

Although the *Equus* comes to life in North America around four and a half million years ago, two million years later it would cross the Bering Straight and expand its horizons into Asia. In this new content a close relative to the *Equus simplicidens* known as the *Equus livenzovensis* would proliferate with tremendous success as it would find suitable habitats from Russia to Spain. It is probable that at the time there were as many as four species of *Equus* representatives in North America. Around one and three-quarter million years ago this variety the *Equus livenzovensis* was overtaken by the *Equus stenosis* as there is stronger evidence of its presence throughout Europe and Asia.

Although the *Hippidion* and *Onohippidium* genera migrated into South America around two and a half million years ago, the representatives of the *Equus* genus did not partake in intercontinental migrations between North and South America until a million and a half years ago. Various species of *Equus* from Europe would also search for new territories in the southern hemisphere. The *Equus numidicus* and *Equus mauritanicus* crossed over to northern Africa and eventually led to the formation of the three zebra species we know today as well as the recently extinguished quagga.

Figure I.17
This table from the Florida Museum of Natural History show the relationship between equid genera and world time periods

Although the asses also had their origins in North America, they eventually would only survive in the central Asia, the Middle East and Africa. This incredibly broad distribution of the *Equus* genera made it one of the most well-distributed and adapted equids in history. During the Pleistocene Epoch at the beginning of Quaternary Period that *Equus* would propagate throughout all the continents except Australia and Antarctica, in varieties that would be better suited to the diverse environments they inhabited. No other genus in the *Perissodactyla* order ever flourished to this degree. Although paleontologists have named hundred of equine species, many of which are the result of incomplete findings, surely there has been much duplicity that has gone undetected. Still, the point is that the sheer richness of palaeontological evidence is surely an indicator of the variety and concentration of equine representatives, most of which correspond to the Pleistocene Epoch between 1.75 million years and 10,000 years ago.

Fossil records during both the Pliocene and Pleistocene indicate that the *Equus* continued to transit back and forth across the Bering land bridge. However, the most notable intercontinental traveler were the "caballine" *Equus* species that made their presence in North America about one and a half million years ago. Around 900,000 years B.P. (before the present) these species crossed over to Asia and spread throughout Eurasia as far as England, Spain and

northern Africa. More importantly, these species may have been recognized as one of the first to take part in backward migrations that took them from Asia back to their origins in North America.

Up until one million years ago, there was a wide variety of one-toed *Equus*, but only a handful of species would make it to historic times. The remaining representatives of the *Equus* genus of our day include: the horse (*Equus caballus*), the taki (*Equus przewalskii*), the onager (*Equus hemionus*), the kiang (Equus kiang) the ass (*Equus asinus*), the mountain zebra (*Equus zebra*), the plains zebra (*Equus quagga*), and the grevy's zebra (*Equus grevyi*). The *Equus przewalskii* and *Equus kiang* have both been the source of disagreements in the field and at different times and by different scientists they have been classified either as separate species or included in the *Equus caballus* and *Equus hemionus* species, respectively. Personally, with their distinct chromosome numbers and phenotypic characteristics I am of the opinion both merit their own specific taxa although staying in the corresponding subgenus of *Equus* and *Hemionus,* respectively. The reader will have to come to his/her own conclusion.
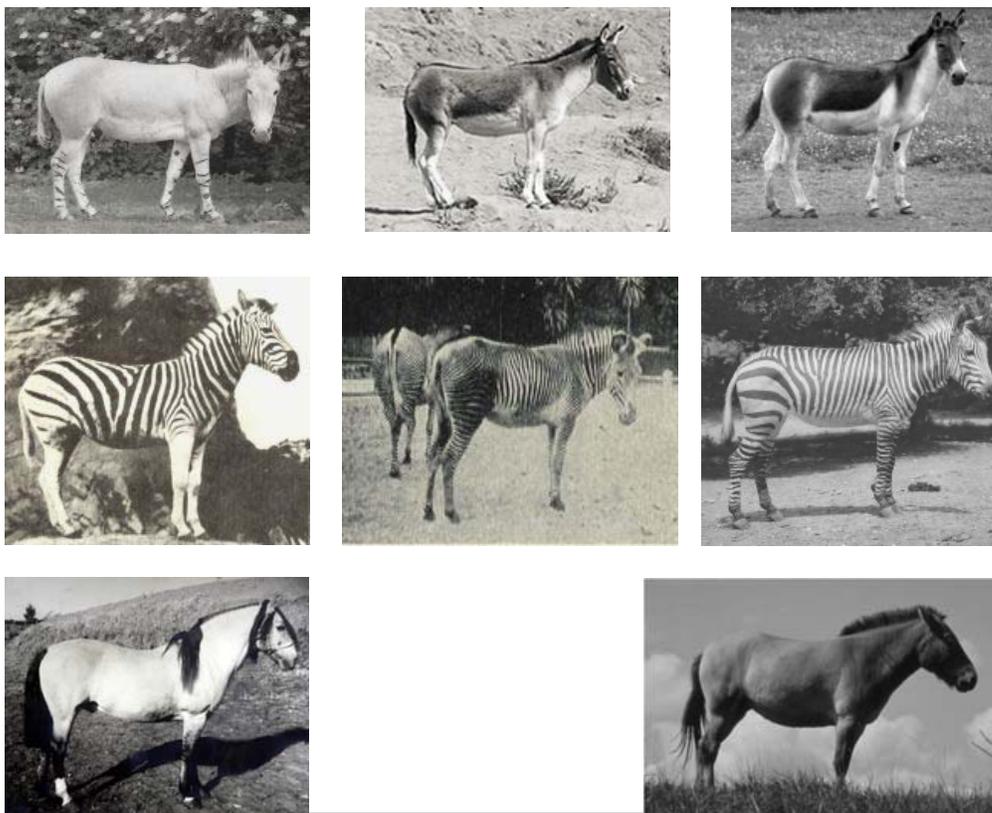

Figure I. 18 - I. 25

a) Equus asinus	b) Equus hemionus	c) Equus kiang
d) Equus quagga	e) Equus grevyi	f) Equus zebra
g) Equus caballus		h) Equus przewalskii

Was it Survival of the Fittest or Survival of the Luckiest?

Modern research has shown the great similarities in the mitochondrial (components of the cytoplasm that are the principal sites for generating energy) DNA of all the Equus species and the quagga from South Africa. In fact, recent research has shown that the DNA of the previously considered independent species "*Equus quagga quagga"* is so like the plains zebra that it is most likely a subspecies. It is important to point out that the quagga was thought of as a

partially striped "ass", while the plains zebra has bold black and white stripes all over its body. Remarkably, the specificity of a subspecies can give rise to considerable phenotypic differences, in spite of the genetic common ground. Such findings exemplify the idea of how an ancestor can branch out into a variety of unique species and subspecies, some of which, like the now extinct quagga, get left by the wayside, while others adapt, mutate or simply luck out enough to survive.

This should make us suspect that nature tossed out many possibilities along the way in evolving the *Hyracotherium* genus into the *Equus* genus. A case in point is the studies we have carried out in this very chapter where we focused on what were traditionally thought to be the ancestors of the *Equus*. Scientific progress has already discarded the direct influence of *Mesohippus*, *Merychippus* and *Pliohippus*. The fact is that recent palaeontological findings have determined that evolution is not a continual straight-line progression from ancestors to eventual descendant. On the contrary, evidence points towards the evolution of many types of

Figure I.26 The *Equus quagga quagga* was determined to be a subspecies of the plains zebra that is also known as *Equus quagga burchelli*

animals who, often by chance, and other times by inflexibility, cease to exist. It is precisely the genetic multiplicity that provides a "shotgun approach" that increases the odds of a particular genus projecting itself into the future.
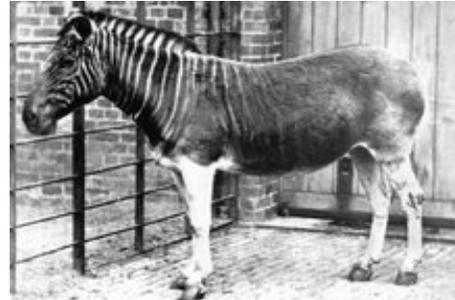
In this regard, modern scientists are refuting the principle of "survival of the fittest" in the absolute sense that was popularized by Charles Darwin. No doubt in some instances this theory has been the reason for the subsistence of a specific genus or species. However, in others, there are logical reasons for the survival of individuals that are less suited to the environment, or in some cases, the continued existence of even the weakest specimens of a group. More contrasting yet is the fact that more times than we care to admit, it is simply the luckiest that have propelled themselves along the evolutionary trail.

For example, in the Eocene period the *Hyracotherium* that originated in the Americas was not the only animal of its type in the world. In Eurasia it gave rise to the first chalicomorph equid, the *Paleotherium,* as well as the *Plagiohippus.* Both thrived simultaneously for a similar number of millions of years as the *Hyracotherium.* Unfortunately, for whatever reason, the climatic changes in the Oligocene period brought them to an evolutionary dead end. One must reason that the cause was not genus specific, as no equid remains have been found in Europe in the late Oligocene rocks.

On the other hand, the *Hyracotherium* is the ancestor to a variety of mammals that evolved in more or less size, more or less dependency on multiple toes, some adapted to browsing and others were better suited to grazing low lying forages. There were many more descendants of the *Hyracotherium* that became extinct than there were those that entered the evolutionary lineage of *Equus.*

For instance, the *Megahippus* developed as a browser in the Old World, but terminated in the Miocene period. The *Parahippus* that would eventually give rise to the first real efficient grazer, the *Merychippus*, also evolved into the chalicomorph body types of the *Hipohippus* and *Anchitherium.* The *Hypohippus* was a large browser that existed in both the Old and New World. They were successful in both continents, yet ceased to exist in the Pliocene Epoch.

While many equids in this period were now grazers depending more solidly on a single digit, the *Anchitherium* still had three toes and survived as yet another unusual example of a long-necked browser that crossed the Bering Strait in late Oligocene times. It branched out into several genera and many species, but still found its demise in Miocenal times.

During the same period in which the *Parahippus* served as a key protagonist in the *Equus* evolution, it also was the direct ancestor of the *Hipparion*, *Neohipparion, Pseudohipparion, Cormohipparion, Merychippus, Nannippus, Pliohippus, Hippidion* and *Onohippidium* all of whom led to dead ends in the evolutionary trail. Some of these smaller Pliocene relatives still had three toes on each foot, but definitely had most of their weight distributed on the central toe.

Both the *Nannippus* and *Neohipparion* came to their evolutionary end in the Americas. The latter existed from 16 to five million years ago, and numerous species have been registered from fossil sites. The *Hipparion* survived by crossing the Bering land route and became one of the most numerous equids between eastern Asia and western Europe. Yet they, too, died out. Finally, the last representatives of the *Hipparion* inhabited Africa alongside other Equidae family until the Pleistocene Epoch, when it is thought they may have been the last of the three-toed equids.

Other *Hipparion* family members, like the *Cromohipparion emsliei*, lasted in North America until two million years ago, while the *Parahipparion* vanished from South America while sharing the transition from Pleistocene to the Holocene Epochs with the *Equus* and *Hippidion*. Fossils estimated to be from 10,080 years B.P. of *Parahipparion saldasi* were found by J. Bird in the Fell Cave of the Magallanes region in southern Chile. In the highlands of central Patagonia in southern Argentina, A. Cardich discovered probable *Parahipparion* fossils in the Los Toldos Cave. At one level, the equid remains were dated at 12,600 +/- 600 years BP, while at shallower levels more of the same evidence showed equids were hunted by the Toldense people that inhabited the cave between 8,750 years B.P. and 11,000 years B.P.

The *Parahippus* went on to give rise to the *Plesshippus* and maybe even the *Dinohippus* itself, but it also was responsible for a remarkably interesting equid that is classified as *Hippidion.* They evolved well after the *Equus*, appearing only around two million years ago. The *Hippidion* was one of the few equids that only existed in South America, and many fossils have been found near Tarija in southern Bolivia. Perhaps the only equid to surpass the *Equus* in size, it is estimated that this browser had the bulk of modern draft horses. Very muscular, with a flat withers and short legs, the *Hippidion* was a unique equid that seemed to have a solid niche in a less competitive part of the Western Hemisphere. They possessed very large and coarse heads with a distinct, very flexible, long Roman nose with corresponding facial fossae. For uncertain reasons they became extinct only around 10,000 years ago, along with all the other equids of the Americas.

The fore-mentioned are only a small portion of the examples of genus that evolved from the *Hyracotherium* that came to a dead end for any one of a variety of reasons already discussed in this chapter. Although the synthesis between *Hyracotherium* and *Equus* seem to point to a chain of events from scansorial equid body forms, to chalicomorphic equid body forms, to a grazing equid body forms, there is no clear cut off point that determines the end of one type and the start of another. Actually, there is a normal overlapping of the body types through the many examples of each that subsist in the same periods of time.

Over and over again, as we look at the descendant of any one genus, we can see diverse body types. Some of these body types toy with drastic new variations that may or may not be suited for the future. Some only slightly alter the mold of the direct ancestor while others are throwbacks to older body types that may find more adaptability with changing conditions. Oftentimes, the body forms that survive carry with them other physiological leftovers from the past that no longer offer advantages.

Conclusion

In the end, the survival of THE species doesn't seem to be a specific objective at all. If it were, how could we explain the fact that most species go extinct? As so often is the case in Nature, order often comes out of chaos. The haphazard results of genetic principles that are based on chance do give rise to more probabilities for the projection of the families of life into the future. Still, there is no getting around the fact that whether the road is long or short, most will be terminal.

It is difficult for us to appreciate this when the window of time in our reality is so limited. Even our accurate sense of history may only be the last few thousand years of a world that clocks its existence in hundreds of millions of years. The hardly conceivable trajectory of the evolution of the *Equus* is a case in point. The past 55 million years can only be comprehended with a deep sense of imagination. Yet even this event is a small part of the two billion year old (2,000,000,000 yrs. is actually a more reasonable *two thousand million years* in most countries

other than the United States that stubbornly holds on to its own, less logical, definition) account of our world.

In spite of the difficulty of visualizing the occurrences over such an incredibly long period of time, I trust that this exercise of learning how the horse evolved has proven informative and interesting. No doubt, archaeological findings in the future will alter some of the conclusions that scientists have made in the present. Just in the course of writing this book I have had to change information which I had originally registered as factual. Some of this information may be viewed in a different light and some may even be proven wrong. Besides, whenever we look this far back in time, there is a good dose of personal opinion in conclusions that are debatable. But, more than the validity of every little detail that is pieced out from million-year-old evidence, we must grasp the importance of realizing how insignificant our role has been in the qualities that define this animal that has captivated us so.

As we look at breeds that men have "created" by applying artificial selection pressures unlike anything seen in nature, it is said that desired results are accelerated a thousandfold. Before we start getting too proud of our accomplishments, we had better realize that those 55 million years that Nature has been at work would be equivalent to changes we could obtain in 55,000 years of controlled breeding. In looking at a mere 6,000 years of equine domestication and less than 2,000 years of planned horse breeding programs, we must humble ourselves to the reality that we are still dealing with one of God's marvelous creations. The raw material that has been molded into a unique **Chilean Horse** breed I will be introducing you to in this book is still the sum total of an infinite number of characteristics that have been developed and tested over time by at least seven genera that paved the way to the Equus. Understanding the origins of these traits and realizing how deeply ingrained they are in the makeup of our modern horse is a responsibility all horsemen have in creating a respectful relationship with the animal that has penetrated furthest into the hearts, minds and accomplishments of mankind.

Figure I.27
Espadachín and Medio Pato are two fine specimens of the Chilean Horse breed, a breed whose type is consistent with the physiological parameters found in the earliest representatives of *Equus caballus* as well as those of most wild species of the *Equus* genus.