HORSE EVOLUTION

by Kathleen Hunt

This is a companion file for the Transitional Fossils FAQ and is part of the Fossil Horses FAQs. In this post I will try to describe the modern view of evolution within the horse family. I apologize in advance for the length; I didn't want to cut it down any more than this, because horse evolution has been oversimplified too many times already. I wanted people to see some of the detail and complexity of the fossil record of a fairly well known vertebrate group. (In fact, even at this length, this post is still only a summary!) People who are in a hurry may just want to read the intro and summary and look at the tree.

Outline

I. Historical Background

In the 1870's, the paleontologist O.C. Marsh published a description of newly discovered horse fossils from North America. At the time, very few transitional fossils were known, apart from Archeopteryx. The sequence of horse fossils that Marsh described (and that T.H. Huxley popularized) was a striking example of evolution taking place in a single lineage. Here, one could see the fossil species "Eohippus" transformed into an almost totally different-looking (and very familiar) descendent, Equus, through a series of clear intermediates. Biologists and interested laypeople were justifiably excited. Some years later, the American Museum of Natural History assembled a famous exhibit of these fossil horses, designed to show gradual evolution from "Eohippus" (now called Hyracotherium) to modern Equus. Such exhibits focussed attention on the horse family not only as evidence for evolution per se, but also specifically as a model of gradual, straight-line evolution, with Equus being the "goal" of equine evolution. This story of the horse family was soon included in all biology textbooks.

As new fossils were discovered, though, it became clear that the old model of horse evolution was a serious oversimplification. The ancestors of the modern horse were roughly what that series showed, and were clear evidence that evolution had occurred. But it was misleading to portray horse evolution in that smooth straight line, for two reasons:

- First, horse evolution didn't proceed in a straight line. We now know of many other branches of horse evolution. Our familiar Equus is merely one twig on a once-flourishing bush of equine species. We only have the illusion of straight-line evolution because Equus is the only twig that survived. (See Gould's essay "Life's Little Joke" in Bully for Brontosaurus for more on this topic.)
- Second, horse evolution was not smooth and gradual. Different traits evolved at different rates, didn't always evolve together, and occasionally reversed "direction". Also, horse species did not always come into being by gradual transformation ("anagenesis") of their ancestors; instead, sometimes new species "split off" from ancestors ("cladogenesis") and then co-existed with those ancestors for some time. Some species arose gradually, others suddenly.

Overall, the horse family demonstrates the diversity of evolutionary mechanisms, and it would be misleading -- and would be a real pity -- to reduce it to an oversimplified straight-line diagram.

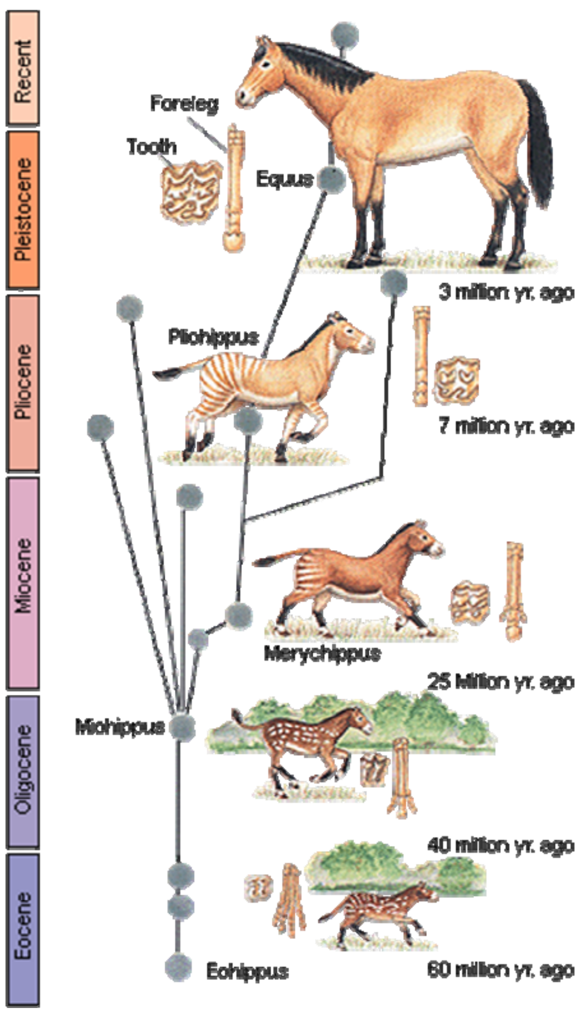
With this in mind, I'll take you through a tour of the major genera of the horse family, Equidae. CAUTION: I will place emphasis on those genera that led to the modern Equus. Do not be misled into thinking that Equus was the target of evolution! Bear in mind that there are other major branches of the horse tree that I will mention only in passing. (See the horse tree for a lovely ASCII depiction.)

Small preface: All equids (members of the family Equidae) are perissodactyls -- members of the order of hoofed animals that bear their weight on the central 3rd toe. (Other perissodactyls are tapirs and rhinos, and possibly hyraxes.) The most modern equids (descendents of Parahippus) are called "equines". Strictly speaking, only the very modern genus Equus contains "horses", but I will call all equids "horses" rather indiscriminately.

Most horse species, including all the ancestors of Equus, arose in North America.

II. Timescale and Horse Family Tree

Recent	10,000 years ago to present
Pleistocene	2.5-0.01 My (million years ago)
Pliocene	5.3-2.5 My
Miocene	24-5.3 My
Oligocene	34-24 My
Eocene	54-34 My



III. Small Eocene Horses

The first equid was Hyracotherium, a small forest animal of the early Eocene. This little animal (10-20" at the shoulder) looked nothing at all like a horse. It had a "doggish" look with an arched back, short neck, short snout, short legs, and long tail. It browsed on fruit and fairly soft foliage, and probably scampered from thicket to thicket like a modern muntjac deer, only stupider, slower, and not as agile. This famous little equid was once known by the lovely name "Eohippus", meaning "dawn horse". Some Hyracotherium traits to notice:

- Legs were flexible and rotatable with all major bones present and unfused.
- 4 toes on each front foot, 3 on hind feet. Vestiges of 1st (& 2nd, behind) toes still present. Hyracotherium walked on pads; its feet were like a dog's padded feet, except with small "hoofies" on each toe instead of claws.
- Small brain with especially small frontal lobes.
- Low-crowned teeth with 3 incisors, 1 canine, 4 distinct premolars and 3 "grinding" molars in each side of each jaw (this is the "primitive mammalian formula" of teeth). The cusps of the molars were slightly connected in low crests. Typical teeth of an omnivorous browser.

At this point in the early Eocene, equids were not yet very different from the other perissodactyl groups; the Hyracotherium genus includes some species closely related to (or even ancestral to) rhinos and tapirs, as well as species that are distinctly equine. [Note: the particular species that probably gave rise to the rest of the equids, H. vassacciense, may be renamed, perhaps to "Protorohippus".]

Though in retrospect we may consider Hyracotherium to be "primitive", it was a very successful animal in its time, and seems to have found a nice stable niche for itself. In fact, throughout most of the Eocene (a good long 20 million years), only minor evolutionary changes took place in Hyracotherium and its near descendants. The body and feet stayed mostly the same, with slight changes in the toes. The major change was in the teeth; as Eocene equids started to eat more plant browse and less fruit, they developed more grinding teeth to deal with the slightly tougher food.

- **Orohippus**

In the early-middle Eocene (approx 50 My), there was a smooth, gradual transition from Hyracotherium to a close relative, Orohippus (MacFadden, 1976). Overall, Orohippus looked much like Hyracotherium: 10-20" high at the shoulder, still "doggish" with arched back, short legs, short neck, short snout, and fairly small brain. Orohippus still had 4 toes on front and 3 behind, with hoofies, and was also "pad-footed". However, the vestiges of the 1st and 2nd toes vanished.

The most significant change was in the teeth. The last premolar changed in shape to become like a molar, giving Orohippus one more "grinding tooth". Also, the crests on the teeth were more pronounced, indicating Orohippus was eating tougher plant material.

- **Epihippus**

Epihippus arose from Orohippus in the middle Eocene (approximately 47 My). Like Orohippus and Hyracotherium, Epihippus was small, doggish, pad-footed, and small-brained, with 4 toes in front and 3 behind. However, tooth evolution was continuing. Now the last two premolars were like molars, giving Epihippus five grinding cheek teeth. The crests on the cheek teeth were well-formed, and still low-crowned.

There is a late form of Epihippus sometimes called Duchesnehippus. It's unclear if this is a subgenus or a species of Epihippus. This animal was basically an Epihippus with teeth similar to, but a bit more primitive than, later Oligocene horses.

IV. Medium-Sized Browsing Horses (Late Eocene & Oligocene)

As we move toward the Oligocene, horses start to change. The climate of North America was becoming drier, and grasses were just evolving. The vast forests were starting to shrink. The late Eocene horses responded by developing tougher teeth and becoming a bit larger and leggier (for better speed out in the open).

- **Mesohippus**

The species Mesohippus celer appears suddenly in the late Eocene, approx 40 My (such sudden speciations can occur when a population encounters new selective forces and/or becomes isolated from the parent species. These speciations are "sudden" only in geological terms, of course, where a few million years is "sudden".) This animal was slightly larger than Epihippus, 24" at the shoulder. It didn't look as doggish, either. The back was less arched, the legs a bit longer, the neck a bit longer, and the snout and face distinctively longer. It had a shallow facial fossa, a depression on the skull. (In later horses these fossae became complex, and handy for species identification.) Mesohippus had three toes on its hind feet and on its front feet -- the 4th front toe was reduced to a vestigial nubbin. As before, Mesohippus was pad-footed. Other significant changes:

- Cerebral hemispheres notably larger -- has distinctly equine brain now.
- Last three premolars are like the three molars, such that Mesohippus (and all later horses) had a battery of six similar grinding "cheek teeth", with one lonely little simple premolar in front.
- Has same tooth crests as Epihippus, well-formed and sharp, more suitable for grinding tougher vegetation.

- **Miohippus**

Soon after Mesohippus celer and its very close relative Mesohippus westoni appeared, a similar animal called Miohippus assiniboiensis arose (approximately 36 My). This transition also occurred suddenly, but luckily a few transitional fossils have been found that link the two genera. A typical Miohippus was distinctly larger than a typical Mesohippus, with a slightly longer skull. The facial fossa was deeper and more expanded. In addition, the ankle joint had changed subtly.

Miohippus also began to show a variable extra crest on its upper cheek teeth. In later horse species, this crest became a characteristic feature of the teeth. This is an excellent example of how new traits originate as variations in the ancestral population.

It was once thought that Mesohippus "transformed" gradually into Miohippus via anagenetic evolution, so that only Miohippus continued. Recent evidence shows that instead, Miohippus speciated (split off) from early Mesohippus via cladogenetic evolution, and then Miohippus and Mesohippus overlapped for some 4 million years. For instance, in one place in modern Wyoming there were three species of late Mesohippus coexisting with two species of Miohippus. (Prothero & Shubin, 1989)

V. The Miohippus Radiation (Early Miocene, 24 My)

Mesohippus finally died out in the mid-Oligocene. Miohippus continued for a while as it was, and then, in early Miocene (24 My) began to speciate fairly rapidly. The horse family began to split into at least 2 main lines of evolution and one small side branch:

- 3-toed browsers called "anchitheres". They were very successful, spread into the Old World, and thrived for tens of millions of years. They retained the small, simple teeth of Miohippus. Genera include Anchitherium and the large Hypohippus and Megahippus.
- A line of small "pygmy horses", e.g. Archeohippus. These horses did not survive long.
- A line that underwent a transformation from browsing to grazing, taking advantage of the new grasses. Large grasslands were just beginning to appear, thus creating a new ecological "opportunity" for grazers. Grass is difficult to chew and wears down teeth rapidly (due to the silica in the leaves) and thus a grass-eater needs tough teeth with ridges of some sort. Open-country grass eaters, in addition, often benefit from being swift runners with long legs. The evolution of this line of horses is described below.

VI. Horses Move Onto the Plains: Spring-Foot & High-Crowned Teeth (Miocene, 18 My)

As this third line of Miocene horses began to specialize in eating grasses, several changes occurred. First, the teeth changed to be better suited for chewing harsh, abrasive grass. Small crests on the teeth enlarged and connected together in a series of ridges for grinding. There was a gradual increase in the height of the tooth crowns, so that the teeth could grow out of the gum continuously as the tops were worn down ("hypsodont" teeth). And, in addition, the tooth crowns became harder due to the development of a cement layer on the teeth.

Second, these horses started to become specialized runners. There was a simultaneous increase in body size, leg length, and length of the face. The bones of the legs began to fuse together, and the leg bones and musculature became specialized for efficient forward-and-back strides, with flexible leg rotation being eliminated. Most significantly, the horses began to stand permanently on tiptoe (another adaptation for speed); instead of walking on doglike pads, their weight was supported by springy ligaments that ran under the fetlock to the big central toe. All these changes occurred rapidly, and we are lucky to have a fairly good fossil record during this time. This was one of the most interesting times in horse evolution. The transitions in these characters are seen in:

- **Kalobatippus**

This genus is not well known, but its teeth seem to be intermediate between Miohippus and the later Parahippus (see below).

- **Parahippus**

Arose in early Miocene, 23 My. A typical Parahippus was a little larger than Miohippus, with about the same size brain and same body form. Parahippus was still three-toed, and was just beginning to develop the springy ligaments under the foot. Parahippus showed gradual and fluctuating changes in its teeth, including the permanent establishment of the extra crest that was so variable in Miohippus. In addition, various other cusps and crests were beginning to join up in a series of strong crests, with slightly taller tooth crowns. Parahippus evolved rapidly and was quickly transformed into a fully spring- footed, hypsodont grazing horse called Merychippus gunteri. This burst of evolution took place about 18-17 My. Later fossils of Parahippus (e.g. the species Parahippus leonensis) are so similar to early Merychippus that it's hard to decide where to draw the line between the genera.

- **Merychippus**

Arose 17 My ago. A typical Merychippus was about 10 hands (40") tall, the tallest equine yet. The muzzle became elongated, the jaw became deeper, and the eye moved farther back, to accommodate the large tooth roots. The brain was notably larger, with a fissured neocortex and a larger cerebellum, making Merychippus a smarter and more agile equine than the earlier horses. Overall, Merychippus was distinctly recognizable as a horse, and had a "horsey" head.

Merychippus was still 3-toed, but was fully spring-footed. This animal stood permanently on tiptoe, supported and propelled by strong, springy ligaments that ran under the fetlock. The side toes were still complete, but began to be of varying sizes; some Merychippus species had full-size side toes, while others developed small side toes that only touched the ground during running. The central toe developed a large, convex, "horsey" hoof, and the legs became longer. The radius and ulna of the forearm fused so that leg rotation was eliminated. Likewise, the fibula of the shin was greatly reduced. All these changes made Merychippus' legs specialized for just one function: rapid running over hard ground.

Merychippus' teeth were fully high-crowned, with a thick layer of cement, and with the same distinctive grazing tooth crests as Parahippus.

Merychippus gunteri evolved into a slightly more advanced form, *Merychippus primus*, in the middle/late Miocene.

VII. The Merychippine Radiation (Miocene, 15 My)

By the late Miocene, Merychippus was the one of the first bona-fide speedy plains grazers. (Simpson, 1961, called Merychippus "the horse with a new look"). Merychippus underwent rapid speciation, and gave rise to at least 19 new grazing horse species in three major groups. This explosive burst of horse evolution is often called the "merychippine radiation". The three major groups were:

1. Three-toed grazers known as "hipparions". These were tremendously successful and split into 4 genera and at least 16 species, eventually covering a variety of niches for small and large grazers and browsers. They developed large and elaborate facial fossae. Hipparions spread from the New World into the Old World in several waves of migration.

2. A line of smaller horses including Protohippus and Calippus, collectively called "protohippines".

3. A line of "true equines" in which the side toes sometimes began to decrease in size. In this flurry of evolution, Merychippus primus gave rise to two later merychippines called M. sejunctus and M. isonesus, who had a mixture of "primitive" (Parahippus-like), hipparion, and equine features. They, in turn, gave rise to M. intermontanus, which begat M. stylodontus and M. carrizoensis. These last two looked quite "horsey" and gave rise to a set of larger three-toed and one-toed horses known as the "true equines" (see below). Crystal clear, right?

As this brief list shows, new species arose in rapid succession in all three of these groups. This rapid speciation makes it hard to determine exactly which species arose from exactly which others.

About 10 My, the horse family reached an apex of diversity (of species and of genera) and sheer numbers which it has never equalled since. The Old and New Worlds both seemed overrun with a wide variety of hipparions, protohippines, and "true equines", large and small, forest browsers and plains grazers. Throughout the evolution of all these related merychippine descendents, the facial fossae got deeper and more elaborate. With so many equine species overlapping at once, these facial fossae may have housed species-specific glands of some sort, similar to the scent- marking glands of modern antelopes and deer.

VIII. One-Toed Horses (Late Miocene, Pliocene & Pleistocene)

Let's leave the hipparions and protohippines now, and concentrate on the merychippine line that led to the "true equines". The late merychippine species of this line, such as M. carrizoensis, were large horses with small side toes. They gave rise to at least 2 separate groups of horses that independently lost their side toes. This occurred as side ligaments developed around the fetlock to help stabilize the central toe during running. These one-toed horses include:

- **Pliohippus**

Arose in middle Miocene (~15 My) as a three-toed horse. Gradual loss of the side toes is seen in Pliohippus through 3 successive strata of the early Pliocene. Pliohippus was very similar to Equus and until recently was thought to be the direct ancestor of Equus, except for two significant differences. First, Pliohippus's skull has deep facial fossae, whereas Equus has no facial fossae at all. Second, Pliohippus's teeth are strongly curved, and Equus's teeth are very straight. Though Pliohippus is obviously related to Equus, it probably didn't give rise to Equus.

- **Astrohippus**

Astrohippus (~10My) was another one-toed horse that arose shortly after Pliohippus. Astrohippus also had large facial fossae, and was probably a descendent of Pliohippus.

- **Dinohippus**

Finally, a third one-toed horse called Dinohippus (recently discovered) arose about 12 My. The exact ancestor of Dinohippus is not yet known (see Evander, 1989). The earliest known species are D. spectans, D. interpolatus, and D. leidyanus. They look smashingly like Equus in foot morphology, teeth, and skull. The teeth were slightly straighter than Merychippus, and the facial fossae were significantly decreased. A slightly later species was D. mexicanus, that showed even straighter teeth and even smaller fossae. Dinohippus was the most common horse in North America in the late Pliocene, and almost certainly gave rise to Equus. (Recall that Equus has very straight teeth and no fossae.)

The Isthmus of Panama arose at this point. Some very early Dinohippus species gave rise to the "hippidions", stocky, short-legged, one-toed horses with odd boxy skulls (~4 My). They travelled into the South America and thrived there briefly.

Throughout the end of the Pliocene, Dinohippus showed a gradual decrease in the facial fossae, straightening of the teeth, and other gradual changes, as Dinohippus smoothly graded into Equus. (Hulbert, 1989)

- **Equus**

Finally we arrive at Equus (4 My), the genus of all modern equines. The first Equus were 13.2 hands tall (pony size), with a classic "horsey" body -- rigid spine, long neck, long legs, fused leg bones with no rotation, long nose, flexible muzzle, deep jaw. The brain was a bit larger than in early Dinohippus. Like Dinohippus, Equus was (and is) one-toed, with side ligaments that prevent twisting of the hoof, and has high-crowned, straight grazing teeth with strong crests lined with cement.

Members of Equus still retain the genes for making side toes. Usually these express themselves only as the vestigial "splint bones" of toes 2 and 4, around the large central 3rd toe. Very rarely, a modern Equus is born with small but fully-formed side toes. (see Gould, Hen's Teeth and Horses' Toes.)

The earliest known Equus species were a set of three "simple Equus" species collectively known as the Equus simplicidens group. They still had some primitive traits from Dinohippus, including a slight facial fossa. They had zebra-like bodies (relatively stocky with a straight shoulder and thick neck), and short, narrow, donkey-like skulls. They probably had stiff, upright manes, ropy tails, medium-sized ears, striped legs, and at least some striping on the back (all traits shared by modern equines). They quickly diversified into at least 12 new species in 4 different groups, in a burst of evolution reminiscent of the great merychippine radiation. All these Equus species coexisted with other one-toed horses (such as Astrohippus) and with various successful hipparions and protohippines, which had been merrily evolving on their own paths.

During the first major glaciations of the late Pliocene (2.6 Ma), certain Equus species crossed to the Old World. Some entered Africa and diversified into the modern zebras. Others spread across Asia, the Mideast, & N. Africa as desert-adapted onagers and asses. Still others spread across Asia, the Mideast, and Europe as the true horse, E. caballus. Other Equus species spread into South America. The Equus genus was perhaps the most successful perissodactyl genus that ever lived -- even before domestication by humans.

Compare Equus to Hyracotherium and see how much it has changed. In no way can Equus and Hyracotherium be considered the same "kind". The change from Hyracotherium to Equus is truly long-term, large-scale evolution.

IX. Modern Equines (Recent)

The three-toed horses gradually died out, perhaps outcompeted by the phenomenally successful artiodactyls (or not). Most of the one-toed horses in North America also died out, as the Ice Ages started. (The causes of these extinctions are unknown.) However, one-toed Equus was very successful. Until about 1 million years ago, there were Equus species all over Africa, Asia, Europe, North America, and South America, in enormous migrating herds that must easily have equalled the great North American bison herds, or the huge wildebeest migrations in Africa.

In the late Pleistocene there was a set of devastating extinctions that killed off most of the large mammals in North and South America. All the horses of North and South America died out (along with the mammoths and saber-tooth tigers). These extinctions seem to have been caused by a combination of climatic changes and overhunting by humans, who had just reached the New World. For the first time in tens of millions of years, there were no equids in the Americas.

The only members of Equus -- and of the entire family Equidae -- that survived to historic times were:

Order Perissodactyla, Family Equidae, Genus Equus

- Equus burchelli: the Plains zebra of Africa, including "Grant's zebra", "Burchell's zebra", "Chapman's zebra", the half-striped Quagga, and other subspecies. The Plains zebra is what people usually think of as the "typical zebra", with rather wide vertical stripes, and thick horizontal stripes on the rump.

- Equus zebra: the Mountain zebra of South Africa. This is the little zebra with the dewlap and the gridiron pattern on its rump.

- Equus grevyi: Grevy's zebra, the most horse-like zebra. This is the big zebra with the very narrow vertical stripes and huge ears.

- Equus caballus, the true horse, which once had several subspecies.

- Equus hemionus: the desert-adapted onagers of Asia & the Mideast, including the kiang (formerly E. kiang).

- Equus asinus: the true asses & donkeys of northern Africa. (The African wild asses are sometimes called E. africanus.)

[I have a separate file about the relationships & current status of all surviving wild equines, including information about captive breeding programs. E-mail for details.]

X. SUMMARY

For many people, the horse family remains the classic example of evolution. As more and more horse fossils have been found, some ideas about horse evolution have changed, but the horse family remains a good example of evolution. In fact, we now have enough fossils of enough species in enough genera to examine subtle details of evolutionary change, such as modes of speciation.

In addition to showing that evolution has occurred, the fossil Equidae also show the following characteristics of evolution:

- Evolution does not occur in a straight line toward a goal, like a ladder; rather, evolution is like a branching bush, with no predetermined goal.

  Horse species were constantly branching off the "evolutionary tree" and evolving along various unrelated routes. There's no discernable "straight line" of horse evolution. Many horse species were usually present at the same time, with various numbers of toes, adapted to various different diets. In other words, horse evolution had no inherent direction. We only have the impression of straight-line evolution because only one genus happens to still be alive, which deceives some people into thinking that that one genus was somehow the "target" of all the evolution. Instead, that one genus is merely the last surviving branch of a once mighty and sprawling "bush".

  The view of equine evolution as a complex bush with many contemporary species has been around for several decades, and is commonly recounted in modern biology and evolution textbooks.

- There are no truly consistent "trends".

  Tracing a line of descent from Hyracotherium to Equus reveals several apparant trends: reduction of toe number, increase in size of cheek teeth, lengthening of the face, increase in body size. But these trends are not seen in all of the horse lines. On the whole, horses got larger, but some horses (Archeohippus, Calippus) then got smaller again. Many recent horses evolved complex facial pits, and then some of their descendants lost them again. Most of the recent (5-10 My) horses were three-toed, not one-toed, and we see a "trend" to one toe only because all the three-toed lines have recently become extinct.

Additionally, these traits do not necessarily evolve together, or at a steady rate. The various morphological characters each evolved in fits and starts, and did not evolve as a suite of characters. For example, throughout the Eocene, the feet changed little, and only the teeth evolved. Throughout the Miocene, both feet and teeth evolved rapidly. Rates of evolution depend on the ecological pressures facing the species.

The "direction" of evolution depends on the ecological challenges facing the individuals of a species and on the variation in that species, not on an inherent "evolutionary trend".

- New species can arise through several different evolutionary mechanisms.

Sometimes, new species split off suddenly from their ancestors (e.g., Miohippus from Mesohippus) and then co-existed with those ancestors. Other species came into being through anagenetic transformation of the ancestor, until the ancestor had changed appearance enough to be given a new name (e.g. Equus from Dinohippus). Sometimes only one or a few species arose; sometimes there were long periods of stasis (e.g. Hyracotherium throughout the early Eocene); and sometimes there were enormous bursts of evolution, when new ecological opportunities arose (the merychippine radiation). Again, evolution proceeds according to the ecological pressures facing the individuals of a species and on the variation present within that species. Evolution takes place in the real world, with diverse rates and modes, and cannot be reduced to a single, simple process.

A Question for Creationists: Creationists who wish to deny the evidence of horse evolution should careful consider this: how else can you explain the sequence of horse fossils? Even if creationists insist on ignoring the transitional fossils (many of which have been found), again, how can the unmistakable sequence of these fossils be explained? Did God create Hyracotherium, then kill off Hyracotherium and create some Hyracotherium-Orohippus intermediates, then kill off the intermediates and create Orohippus, then kill off Orohippus and create Epihippus, then allow Epihippus to "microevolve" into Duchesnehippus, then kill off Duchesnehippus and create Mesohippus, then create some Mesohippus-Miohippus intermediates, then create Miohippus, then kill off Mesohippus, etc.....each species coincidentally similar to the species that came just before and came just after?

Creationism utterly fails to explain the sequence of known horse fossils from the last 50 million years. That is, without invoking the "God Created Everything To Look Just Like Evolution Happened" Theory.

[And I'm not even mentioning all the other evidence for evolution that is totally independent of the fossil record -- developmental biology, comparative DNA & protein studies, morphological analyses, biogeography, etc. The fossil record, horses included, is only a small part of the story.]

Truly persistent and/or desperate creationists are thus forced into illogical, unjustified attacks of fossil dating methods, or irrelevant and usually flat-out wrong proclamations about a supposed "lack" of "transitional forms". It's sad. To me, the horse fossils tell a magnificent and fascinating story, of millions of animals living out their lives, in their natural world, through millions of years. I am a dedicated horse rider and am very happy that the one-toed grazing Equus survived to the present. Evolution in no way impedes my ability to admire the beauty and nobility of these animals. Instead, it enriches my appreciation and understanding of modern horses and their rich history.

- *"All the morphological changes in the history of the Equidae can be accounted for by the neo-Darwinian theory of microevolution: genetic variation, natural selection, genetic drift, and speciation." (Futuyma 1986, p.409)*

- "Because its complications are usually ignored by biology textbooks, creationists have claimed the horse story is no longer valid. However, the main features of the story have in fact stood the test of time...." (Futuyma 1982, p. 85)

- "When asked to provide evidence of long-term evolution, most scientists turn to the fossil record. Within this context, fossil horses are among the most frequently cited examples of evolution. The prominent Finnish paleontologist Bjorn Kurten wrote: 'One's mind inevitably turns to that inexhaustible textbook example, the horse sequence. This has been cited -- incorrectly more often than not -- as evidence for practically every evolutionary principle that has ever been coined.' This cautionary note notwithstanding, fossil horses do indeed provide compelling evidence in support of evolutionary theory." (MacFadden 1988, p. 131)

- "The fossil record [of horses] provides a lucid story of descent with change for nearly 50 million years, and we know much about the ancestors of modern horses." (Evander 1989, p. 125)

- "It is evolution that gives rhyme and reason to the story of the horse family as it exists today and as it existed in the past. Our own existence has the same rhyme and reason, and so has the existence of every other living organism. One of the main points of interest in the horse family is that it so clearly demonstrates this tremendously important fact." (Simpson, 1961, p. xxxiii)

XI. References

I've tried to incorporate all the recent research I could find into this post. For more information, non-scientists may want to start with Simpson's 1961 book, Horses. This book is a classic, readable account of horse evolution, and though it's now somewhat outdated, I think it's still the most accessible introduction to the topic. However, I strongly recommend that Simpson's book be supplemented with newer information from MacFadden's (1988) nice summary and/or Prothero & Schoch's The Evolution of Perissodactyls (1989). These and other selected references are listed below.

Thanks to Larry Moran for the prototype of the ASCII horse tree and other various notes.

Bennett, D.K. 1986? (year not on my xerox! argh.) The origins of breeds. Equus 110:33, 11:37, 112:37. (This is a three-part series in a good-quality trade magazine, written for horse owners who have some interest in science and evolution. (Further references are in the articles.) The author is a vertebrate paleontologist who specializes in the evolution, form, and function of modern Equus. Her analysis shows that E. caballus had at least 5 subspecies before domestication.)

Colbert, E.H. 1980. Evolution of the Vertebrates, 3rd edition. John Wiley & Sons, New York. Carroll, R.L. 1988. Vertebrate Paleontology and Evolution. WH Freeman & Co., New York. (These are two standard texts on vertebrate fossils & evolution. Colbert has a 4th edition out now.)

Futuyma, D.J. 1982. Science on Trial: The Case for Evolution. Pantheon Books, New York. (A well-written book on the evidence for evolution, written for the layperson.)

Futuyma, D.J. 1986. Evolutionary Biology. Sinauer Associates, Sunderland, Mass. (A standard text covering theories of how evolution occurs -- doesn't stress evidence for evolution per se.)

Gould, S.J. 1983. Hen's Teeth And Horse's Toes. Gould, S.J. 1991. Bully for Brontosaurus. (Collections of essays written for Natural History magazine. "Hen's Teeth..." has essays on horse side toes and zebra stripes; "Bully..." contains essays on "fox-terrier size" Hyracotherium and on the fallacy of perceiving a direction of evolution in the horse family. Other essays are interesting too.)

Hildebrand, M. 1987. The mechanics of horse legs. Amer. Sci. 75:594-601. (Not about evolution, but interesting & useful nonetheless.)

Janis, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution 30:757-774. (An interesting analysis of the significance of hindgut fermentation in equids, and on why the Equidae tend not to have high species diversity.)

Lowenstein, J.M., and O.A. Ryder. 1985. Immunological systematics of the extinct quagga (Equidae). Experientia 41:1192-1193. (The authors studied molecules from skins of the extinct quagga, and conclude it was a subspecies of the plains zebra.)

MacFadden, B.J. 1976. Cladistic analysis of primitive equids with notes on other perissodactyls. Syst. Zool. 25(1):1-14. (An analysis of the interrelationships of Hyracotherium, Orohippus, Epihippus, the paleotheres, and other early perissodactyls.)

MacFadden, B.J. 1984. Systematics and phylogeny of the Hipparion, Neohipparion, Nannippus, and Cormohipparion (Mammalia, Equidae) from the Miocene and Pliocene of the New World. Bull. Am. Mus. Nat. Hist. 179:1-196. (Extremely detailed analysis of evolution and interrelationships of the hipparions. [Okay, okay, I didn't read the whole thing.] Relies to a large extent on the distinctive morphology of the facial fossae in different species.)

MacFadden, B.J. 1984. Astrohippus and Dinohippus from the Yepomera local fauna (Hemphillian, Mexico) and implications for the phylogeny of one-toed horses. J. Vert. Paleon. 4(2):273-283. (Description & discussion of Pliohippus, Astrohippus, and Dinohippus. Concludes that Dinohippus was probably the ancestor of Equus, and Pliohippus was probably the ancestor of Astrohippus.)

MacFadden, B.J. 1985. Patterns of phylogeny and rates of evolution in fossil horses: hipparions from the Miocene and Pliocene of North America. Paleobiology 1(3):245-257. (Analyzes the evolution of hipparion species. Of the 16 known species, 6 appear too suddenly for the mode of speciation to be determined. Of the 10 that appeared gradually enough for speciation mode to be determined, 5 have originated by anagenesis (transformation of an ancestor species into a descendent species, such that the ancestor "disappears") and 5 by cladogenesis (splitting off of a new species from an ongoing ancestor species, such that the 2 species continue to exist together.))

MacFadden, B.J. 1986. Late Hemphillian monodactyl horses (Mammalia, Equidae) from the Bone Valley formation of central Florida. J. Paleontology 60(2):466-475. (Description of two recent discovered advanced one-toed horse species: Astrohippus stocki and Dinohippus mexicanus.)

MacFadden, B.J. 1988. Horses, the fossil record, and evolution: a current perspective. Evol. Biol. 22:131-158. (A useful and readable update on current evidence & theories of horse evolution.)

MacFadden, B.J. 1993. (A new book about horse evolution. I have not read it yet but am trying to get a copy. Over $70! sheesh.)

MacFadden, B.J., J.D. Bryant, and P.A. Mueller. 1991. Sr-isotopic, paleomagnetic, and biostratigraphic evidence of horse evolution: evidence from the Miocene of Florida. Geology 19:242-245. (This is an interesting example of the variety of dating methods paleontologists use to date their finds. MacFadden et al. dated the Parahippus to Merychippus transition at a Florida site with paleomagnetic data and Sr/Sr dates, and also by cross-correlation to other sites dated with Sr/Sr, K/Ar, Ar/Ar, zircon fission-track, and paleomagnetic dating methods. Surprise, surprise, all the dates were consistent at roughly 16 My.)

MacFadden, B.J., & R.C. Hubbert. 1988. Explosive speciation at the base of the adaptive radiation of Miocene grazing horses. Nature 336:466-468. (An interesting summary of the merychippine radiation. Has a nice horse tree, too. MacFadden's horse tree is used by almost everyone these days.)

MacFadden, B.J., & M.F. Skinner. 1981. Earliest holarctic hipparion, Cormohipparion goorisi n.sp. (Mammalia, Equidae) from the Barstovian (medial Miocene) Texas gulf coastal plain. J. Paleontology 55(3):619-627. (Description of a hipparion that was found to have crossed into the Old World from the New World sooner than previously realized.)

Prothero, D.R., & R.M. Schoch, eds. 1989. The Evolution of Perissodactyls. Clarendon Press, New York. (A compilation of current research and theories of perissodactyl evolution. The following chapters were particularly useful:

Evander, R.L. Phylogeny of the family Equidae. pp. 109-126

MacFadden, B.J. Dental character variation in paleopopulations and morphospecies of fossil horses and extant analogs. pp. 128-141

Hulbert, R.C. Phylogenetic interrelationships and evolution of North) American late Neogene Equinae. pp. 176-196.

Prothero, D.R., & R.M. Schoch. Origin and evolution of the perissodactyla: summary and synthesis. pp. 504-529.

Prothero, D.R., & N. Shubin. The evolution of Oligocene horses. pp.142-175.

Winans, M.C. A quantitative study of North American fossil species of the genus Equus. pp. 262-297.)

Radinsky, L. 1983. Allometry and reorganization in horse skull proportions. Science 221 (16 Sept):1189-1191 (Analysis of horse skull changes around the time that horses developed high-crowned teeth, between 15 and 25 million years ago.)

Renders, E. 1984. The gait of Hipparion sp. from fossil footprints in Laetoli, Tanzania. Nature 308:179-181. (Interesting paper describing fossil hoofprints of an adult female hipparion and her foal. They were using a gait called a "running walk".)

Simpson, G.G. 1961. Horses. Doubleday & Co., New York. (An interesting and readable, though outdated, account of horse evolution. Written for the intelligent non-scientist by a prominent paleontologist.)

Thomason, J.J. 1986. The functional morphology of the manus in the tridactyl equids Merychippus and Mesohippus: paleontological inferences from neontological models. J. Vert. Pal. 6(2):143-161. (Analysis of the pad-foot to spring-foot transition.)

"[Fossils] are animals, just as full of life as you are, even though they occur at different points in the endless stream of time. Within their own segments of this stream, they breathe, eat, drink, breed, fight, and live their own lives..." (Simpson, 1961, p. xxxiv)