

Phylogeny of the horse—from tapir-like hyracotheres or from equine anchitheres?

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Model-driven interpretation of fossil evidence has led to specious placement of hyracotheres within the horse family. Instead hyracotheres and other Eocene hyracothere-like animals, generally considered to be primitive members of various perissodactyl groups, are interpreted here to constitute a monophyletic family that is phylogenetically independent of the majority of other perissodactyls. Fossil horses are first represented by the anchithere *Mesohippus* in the Eocene strata. Attempts to link the anchitheres (browsing horses) to the hyracotheres are speculative and insufficiently supported by fossil evidence. Therefore, inclusion of the separate subfamily Hyracotheriinae within the Equidae makes the family polyphyletic. A second question, whether the Anchitheriinae represent a separate monophyletic group independent of the Equinae, remains unresolved. Fossil morphological criteria suggest the entire anchithere–equine group is a monophyletic family. The main difference between the anchithere and the equine fossils lies in the teeth, in the characteristic hypsodontic state of the later. The transition from brachydonty to hypsodonty appears to have occurred within a single equine genus *Merychippus*.

Horses have accompanied man since the earliest human civilizations^{1,2} and fossil horses bring fascinating insights into paleontology.³ Since Thomas Huxley gave them a place of prominence, fossil horses and their phylogeny have been an icon of evolution (figure 1). As investigations of the fossil record have become more data-driven rather than hypothesis-driven, our understanding of the evolution of the horse has mellowed. At the very bottom of traditional horse phylogenies is found that curious animal *Hyracotherium* (figure 2), also known by its famous junior synonym ‘*Eohippus*’, and it is accompanied by various similar organisms. The genus *Hyracotherium* comprises a number of separate species and it existed alongside a number of related genera. In horse phylogenies, gaps exist, some more prominent than others. This paper examines the most prominent gap which separates the Eocene hyracotheres from the horses. It looks at whether horse phylogeny began with *Hyracotherium* or with *Mesohippus*, a Miocene three-toed browsing horse. A second accompanying paper will examine the relationship of hyracotheres with other early Perissodactyla. Given that speciation has occurred among extinct and extant horses, the role of adaptive radiation and the types of morphogenetic change involved are also examined.

Extant horses, asses, and zebras clearly belong to a single basic type.⁴ The rapid karyotype rearrangements of *Equus*⁵ and the extensive equid fossil record mostly confirm a monophyletic origin of the family but what about *Eohippus* and the other hyracotheres? Other important questions include: Which fossils belong to which basic type? What are limits of the morphogenetic potential displayed by the

different basic types? Can alternative dentitions be attributed to genetic and epigenetic potential of a single basic type? Can one-toed and three-toed horses belong to a single basic type? Within a basic type all species are related to one another reproductively. Per definition, fossil species must be excluded from basic types, as far as empirical evidence is concerned. Therefore, two taxa are recognized: the basic type, which is a functional concept based on reproduction, and a family or created kind, which includes all species that share a common genetic ancestry. The latter is a theoretical concept, though still based on reproduction. It represents a family of organisms in the true sense of the meaning. It assumes the history of life is polyphyletic, with multiple trees of life (i.e. sylvan not monoarboreal—a forest of separate family trees rather than a single tree of life). Each tree is a family of related organisms comprising one or more basic types, depending on reproductive isolation of extant member species.

Because hybridization events between extinct species are usually impossible to assess, basic type categorization of fossils employs an alternative approach, one based on morphogenetic space as evidenced by documented hybridizations between member species. If the phenotype of a fossil falls within this space, inclusion within the basic type is considered appropriate. If the phenotype of a fossil falls outside this space, but within a basic type’s reasonable morphogenetic potential, inclusion within the basic type is still indicated. If the phenotype of a fossil falls within the morphogenetic potential of a basic type, but displays a limited number of characters used to define organisms outside the basic type, inclusion within the basic type is

indicated and the reliability of the defining characters is questioned. Morphometric criteria are used to empirically delineate a morphogenetic space defined by hybridizations. If such principles cannot be applied, ‘unspecified basic type’ status must necessarily be retained even though classification into higher taxa, including the family, may still be undertaken using alternative criteria.

Does the evolution of the horse begin with *Hyracotherium*?

In this section the question is addressed; whether *Hyracotherium* and related fossils should be included within the horse family. See table 1 for a listing of the horse genera discussed.

In his time, Sir Richard Owen was the foremost zoologist in England and founded the Natural History Museum in London. He was certainly one of the best people to appreciate what it meant when the fossil remains of an unknown beast were given to him by natural history enthusiast William Richardson, who had been collecting specimens from the coast of Kent in 1839. The piece was the front half of a little skull, and the large eyes and short snout gave the initial impression of it being a hare or rodent. However, a close inspection of the teeth, with their cusps and ridges, indicated that it was an ungulate, one of the hoofed mammals. There were similarities to the rodent-like but ‘hoofed’ hyrax and shortly afterwards Sir Richard christened the fossil *Hyracotherium*, the “hyrax beast”.⁶ Had there been any clear similarity to fossil horses, Sir Richard would certainly have been aware of it. He had recently described a Pleistocene horse whose fossil remains had been brought from Argentina on the HMS Beagle by Charles Darwin,⁷ and he subsequently went on to name the fossil equine genus *Hippidion*.⁸ In 1851, Owen even suggested an orthogenetic horse

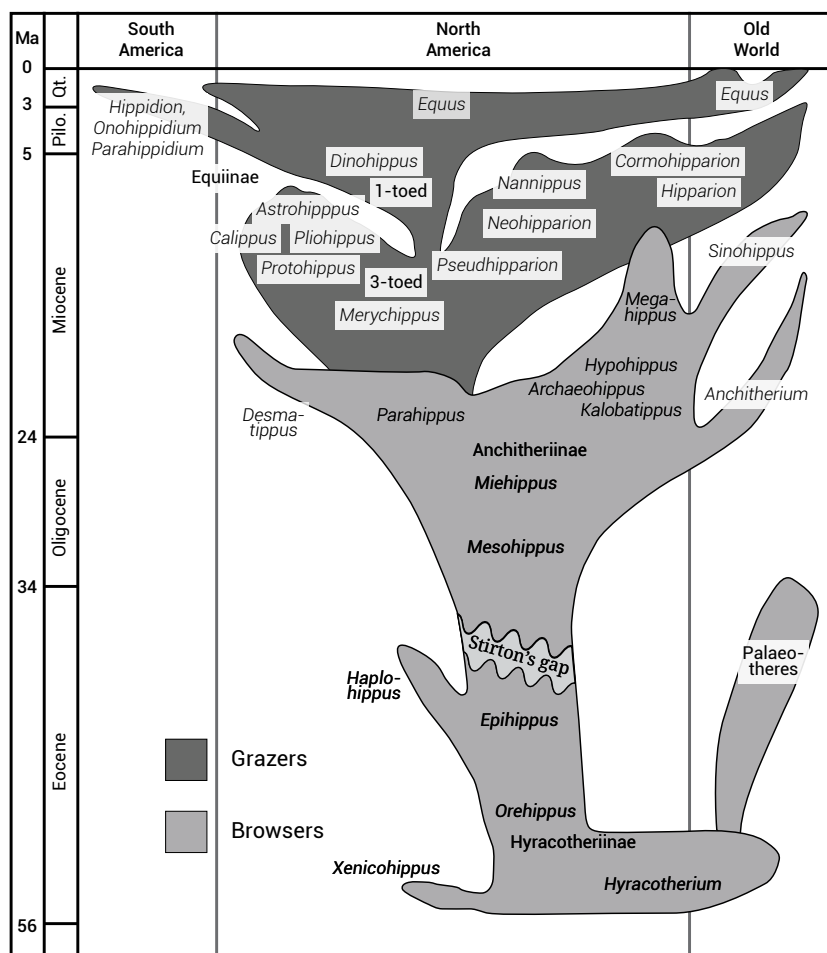


Figure 1. Standard phylogeny of the Equidae; after MacFadden.³ A gap is indicated between the Hyracotheriinae and the Anchitheriinae. This gap is discussed in detail in the text. Sturton noted in his phylogeny at the site of this gap: “Intergradation between *Epihippus* and *Mesohippus* not proved”.³⁷

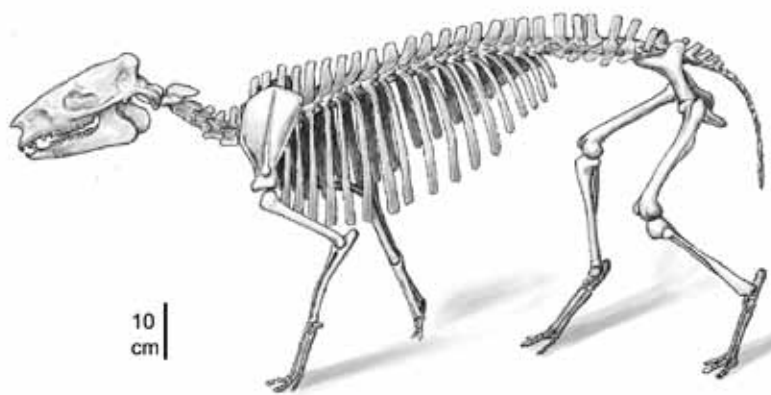


Figure 2. Skeleton of *Hyracotherium vasaccense*, from Lower Eocene strata, North America. This was a large hyracothere, the size and weight of a German shepherd dog. The smallest hyracothere, *H. sandrae*, was the size of a domestic cat and comparable to Sir Richard Owen’s ‘hyrax beast’, *H. leporinum* (MacFadden³). Drawing by R.W. Sanders.

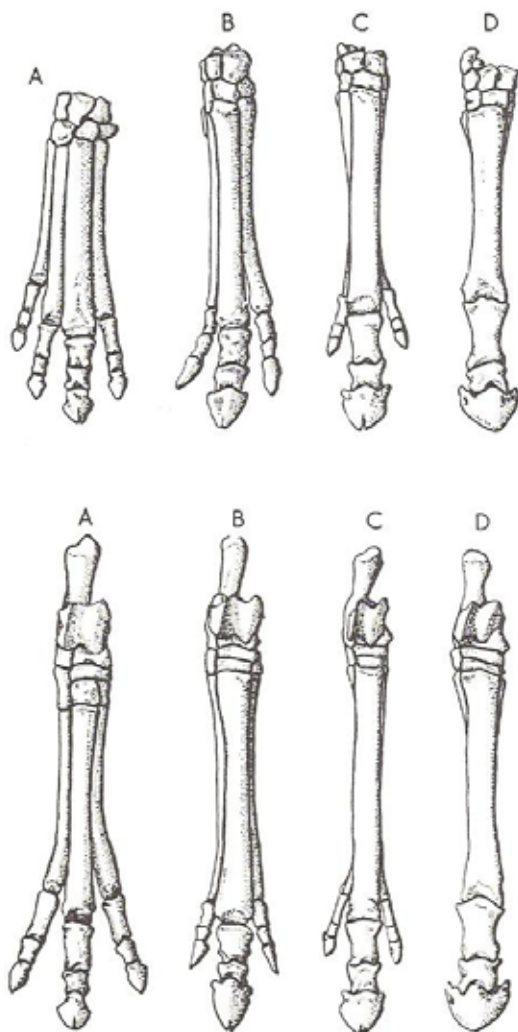


Figure 3. Comparative sequence of feet of Equidae: manus (front foot) above, pes (back foot) below; after Romer.²⁴ The front feet demonstrate the four-toed splayed foot of *Hyracotherium* compared with the feet of various horses, with their prominent weight-bearing middle toe; see text for details. A) *Hyracotherium*, Lower Eocene; B) *Miohippus*, Oligocene; C) *Merychippus*, Upper Miocene; D) *Equus*, present. Figures not to scale.

sequence starting with *Palaeotherium* (with its three-toed feet) and ending with *Equus*,^{9,10} of particular note here because he chose not to include *Hyracotherium*.

Thomas Huxley, a junior contemporary of Owen's, believed deeply in Darwin's ideas and in 1872 he proposed that three fossil ungulates, *Palaeotherium*, *Anchitherium* and *Hipparion*, if placed in order of their stratigraphic appearance, charted an evolutionary path to the modern horse *Equus*. The idea had originated from Owen⁷ and was reasonable, except for *Palaeotherium*, which was clearly tapir-like (see next paragraph). The interpretation was hypothesis-driven rather than data-driven. The original phylogeny already contained two remarkable horse fossils. *Anchitherium* was an early Miocene three-toed browsing

horse and *Hipparion* was a late Miocene three-toed grazing horse. What was still needed was an animal that was less horse-like, more 'dawn-mammalian', and ideally from the early Eocene. *Palaeotherium*, located in middle and late Eocene strata in Europe, seemed to fit the bill very well.¹¹

Palaeotherium was described by Baron Georges Cuvier.¹² It was one of the first fossil mammals to be documented and its remains had been unearthed from gypsum deposits around Montmartre in Paris. It was about the size of a cow and had big heavy bones and broad, three-toed feet with hooves. Its limbs were suitable for walking about in heavy underbrush and wading through swampy ground, rather like a modern tapir. It had a somewhat tapir-like head and a deep notch in the nasal bones, indicating muscle attachments for a tapir-like proboscis.¹¹ Although not considered a tapir, primarily because of its dental pattern, it was thought to look very similar to one. Instead, it is placed in a separate family, the Palaeotheriidae. Another European Eocene fossil, *Pachynolophus* (synonym *Orohippus*) *agilis*, was subsequently inserted at the front of Owen's original horse phylogeny by Gaudry.¹³ This beast was more tapir-like and had a four-toed forelimb (tetradactyl manus) and a three-toed hindlimb (tridactyl pes) like *Hyracotherium* (figures 3 and 4). The name *Orohippus agilis* had already been used by Marsh for an American Eocene fossil with tetradactyl manus and tridactyl pes, that was similar to *Hyracotherium*, and which he had placed at the front of his own horse phylogeny.¹⁴ Yet another Eocene fossil *Protorohippus*, with tetradactyl manus and tridactyl pes and also closely related to *Hyracotherium*, was also placed into a horse phylogeny by Matthew.¹⁵

Huxley's original phylogeny included not only *Palaeotherium* but two three-toed horses, *Anchitherium* and *Hipparion*. Because modern horses are usually one-toed (monodactyl) this will have come as a surprise to some. However, modern horses with partially developed side toes are by no means unknown. They are referred to as 'horned horses'. It appears to be an inherent part of the morphogenetic potential of the horse. They can form side toes either by excessive embryogenic development of the normally vestigial, lateral toes or duplication of the existing, central toe.¹⁶ The genetic potential of modern horses includes both one-toed and three-toed phenotypes. At least in times past, this apparently enabled the equid basic type to selectively adapt to different ecological habitats. During the middle and late Tertiary, when major horse radiations took place, extra toes would have given better traction on the softer, often marshy, ground (figure 5). The poorly diversified humid forests of the early Tertiary matured into more complex deciduous rainforests, and with the cooling and drying of the climate during the Oligocene and Miocene this biome was replaced by open forest

savanna and grassland savanna.^{17,18}

As a result, the dominance of early browsing horses gave way to grazing species. In terms of number of species, the three-toed horses were certainly very successful. However, as the great plain ecosystems developed into vast expanses of open, firm land the one-toed horses, generally of greater size and speed, finally began to dominate.³

The origin of the iconic series of fossil horses

In 1876, during the centennial celebrations in the United States, Thomas Huxley came to hold a series of lectures and to present his ideas on the evolution of the horse. He visited Yale and spent two days with Othniel

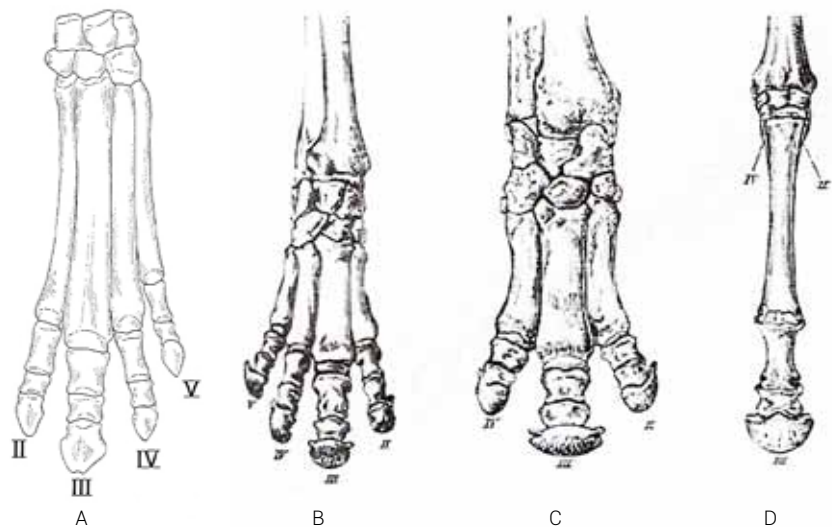


Figure 4. Comparison of forefoot of *Hyracotherium* with those of three extant families of perissodactyls; after Romer,²⁴ and Flower.⁴⁷ A: *Hyracotherium*; B: Tapir (*Tapir indicus*); C: Rhinoceros (*Dicerorhinus sumatrensis*); D: Horse (*Equus caballus*). Roman numerals indicate homology of digits. Figures are not to scale.

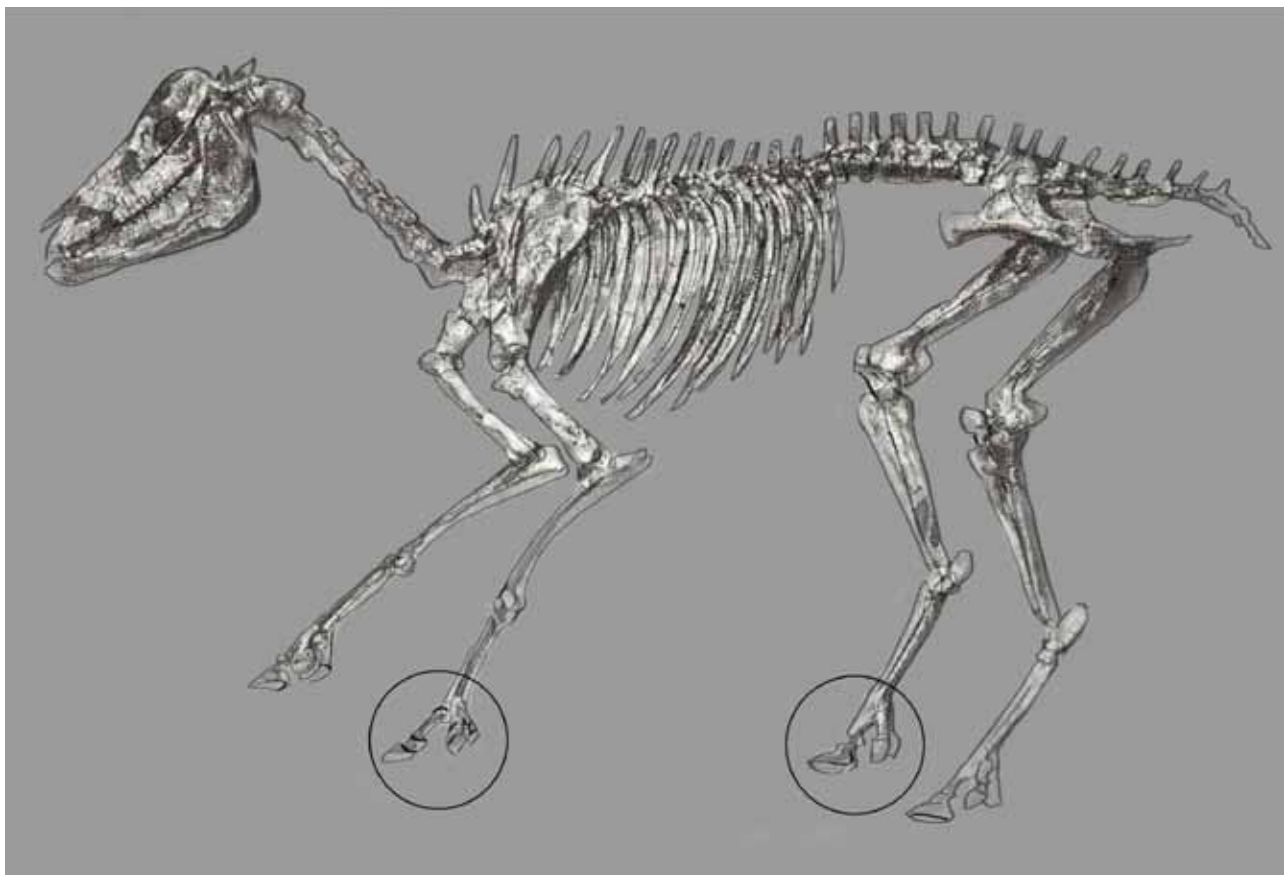


Figure 5. Sketch of the matrix-bound skeleton of *Hipparion*, one of many three-toed Equinae, from Miocene deposits at Höwenegg, Germany; after MacFadden.³ The skeleton emphasizes the manner in which the lateral toes are being used for back support for the main weight-bearing central toe. This is in stark contrast to the way the four toes of hyracotheres and extant tapirs form a splayed foot (see figures 3 and 4). The feet are adapted to different kinds of needs in different terrains.

Table 1. Interrelationships among the Equidae (after MacFadden³).

Family	Subfamily	Genera cited in text [synonyms]
Equidae	Hyracotheriinae (taxonomic position disputed here)	<i>Propalaeotherium</i>
		<i>Eurohippus</i>
		<i>Hallensia</i>
		<i>Hyracotherium</i> [<i>Eohippus</i> , <i>Pliolophus</i> , <i>Orohippus</i>]
		<i>Xenicohippus</i>
		<i>Protorohippus</i>
		<i>Orohippus</i> [<i>Pachynolophus</i>]
		<i>Haplohippus</i>
		<i>Cymbalophus</i>
		<i>Epihippus</i>
	Anchitheriinae	<i>Mesohippus</i>
		<i>Miohippus</i>
		<i>Kalobahippus</i> [<i>Anchitherium</i>]
		<i>Anchitherium</i>
		<i>Sinohippus</i>
		<i>Hypohippus</i>
		<i>Megahippus</i>
		<i>Archaeohippus</i>
	Equinae	<i>Desmatippus</i>
		<i>Parahippus</i>
		<i>Merychippus</i>
		<i>Parahippus</i>
		<i>Pliohippus</i>
		<i>Calippus</i>
		<i>Nannippus</i>
		<i>Hipparion</i>
		<i>Neohipparion</i>
		<i>Hippidion</i>
		<i>Dinohippus</i>
		<i>Equus</i>

Marsh. Marsh, spurred on by his ‘bone war’ with Edward Cope, had collected large numbers of North American fossil specimens including many horse species. He had found what he considered to be Eocene horses in the Rocky Mountains. Some three years before, Cope had described what he considered might be ‘horse’ specimens, recovered from

early Eocene beds in Wyoming, naming them *Eohippus*, ‘dawn horse’.¹¹ Nevertheless, the genus name is attributed to Marsh.¹⁹ Cope recognized *Eohippus* was the American equivalent of *Hyracotherium* but still placed it at the base of the American horse phylogeny. When Huxley discussed these matters with Marsh, he was delighted. The American sequence contained two hyracotheres, two browsing horses, and two grazing horses. Huxley considered this American sequence: *Eohippus*-*Orohippus*-*Mesohippus*-*Miohippus*-*Pliohippus*-*Equus* to be superior to the European sequence: *Palaeotherium*-*Anchitherium*-*Hipparion*-*Equus*. No doubt a break with the horse sequence of Owen, with whom he had a long-standing personal grievance,¹⁰ was also welcome. Huxley adopted it for his series of lectures and it has become an icon of evolution ever since. These genera are described in more detail below.

Besides *Equus*, the American sequence contains a grazing horse (subfamily Equinae) with both three-toed and one-toed species, *Pliohippus*.³ The sequence also contains two browsing horses (subfamily Anchitheriinae), *Mesohippus* and *Miohippus*. These sister genera, which had overlapping temporal and geographic ranges, did not intergrade but from their earliest appearance formed distinct horse genera.²⁰ They are related to the European *Anchitherium*. The sequence also contains the four-toed *Orohippus*, a close relative of *Hyracotherium*, and *Eohippus*, which is so similar to the European *Hyracotherium* that both Cooper²¹ and Simpson²² argued they are congeneric. This means the name ‘*Eohippus*’ is an invalid junior synonym of *Hyracotherium*.²³ Owen never considered *Hyracotherium* a horse. It was about the size of a domestic cat. It had a long, flexible back with a long bony tail. It possibly ran a little like a rabbit. Examination of perissodactyl dental patterns (figure 6) clearly and incontrovertibly reveals the similarities in dentition between *Hyracotherium* and a contemporary early Eocene genus *Homogalax*.^{20,24,25}

Recent studies by Hooker^{26,27} have resulted in a paradigm shift in interpretation of *Hyracotherium* fossils. He considered them to include a whole variety of closely related species, which gave rise to prominent branches of the perissodactyl order. Owen’s species gave rise to the palaeotheres. Marsh’s species gave rise to the brontotheres. Yet another species, to which Owen²⁸ had given the genus name *Pliolophus* (considered a synonym of *Hyracotherium*), gave rise to the horses. This novel interpretation aside, there seems little doubt that the Anchitheriinae—*Anchitherium*, *Mesohippus* and *Miohippus*—were browsing horses and part of a major horse radiation during the middle Tertiary.²⁰ *Hyracotherium* and *Orohippus* appear part of another story and to understand this we must take a closer look at the perissodactyls.

The discussion so far suggests that the horse basic type includes two subfamilies—the browsing horses (Anchitheriinae) and the grazing horses (Equinae). The third subfamily, the hyracotheres (Hyracotheriinae), appears to encompass a different kind of animal and includes *Eohippus* (=Hyracotherium).

Does the evolution of the horse begin with the browsing anchitheres?

In this section we discuss the questions: Are the browsing horses the first true horses observed in the fossil record, and does an unbroken line of fossil evidence exist indicating that browsing horses (Anchitheriinae) and grazing horses (Equinae) belong to the same family (created kind)? See table 1 for a listing of horse genera discussed.

Fossils of browsing horses appear in the late Eocene strata of North America (*Mesohippus*) and the Miocene of Europe and Asia. MacFadden^{3,18,23} emphasizes that genera within the subfamily Anchitheriinae (browsing horses) are set apart from the hyracotheres by at least seven synapomorphies including those of the skull, jaws, dentition, and metapodials (the bones of feet). The cheek teeth of all the anchitheres are typically horse-like, being fully and characteristically molarized.²⁰ The preorbital skull length is expanded (the long horse-like muzzle). The upper leg segments are longer, as well as the toes, once again typical of horses, and the anchitheres are functionally tridactyl in both manus and pes.

The Anchitheriinae include the genera *Mesohippus*, *Miohippus*, *Kalobatippus*, *Hypohippus*, *Megahippus*, *Archaeohippus*, *Desmatippus*, *Parahippus*, *Anchitherium*, and the Chinese *Sinohippus*.²⁵ *Anchitherium* was so common in France that it was one of the first fossil mammals ever found. *Mesohippus* and *Archaeohippus* were both dwarf forms. *Hypohippus* and *Megahippus*, however, were large horses comparable in size to many extant species of horse. During the adaptive radiation of the anchitheres, body size potential was thoroughly explored. The Equinae (grazing horses) appeared possibly as a result of an adaptive radiation from *Parahippus*.³ Extensive radiations of the Equinae took place as grasslands developed. It is reasonable to assume that these creatures through their grazing habits literally carved out their own habitat replacing forested savanna with grassland savanna and steppe. When one considers the enormous size of the buffalo herds on the prairies described by early European settlers, it is not difficult to imagine how equine herds of similar magnitude would have helped sculpt these vast grasslands.¹¹

Advanced species of the anchithere *Parahippus* and subsequent equine genera displayed a dental feature that made their teeth more durable. It was cement, a bone-like mineral substance that forms a protective cap around the

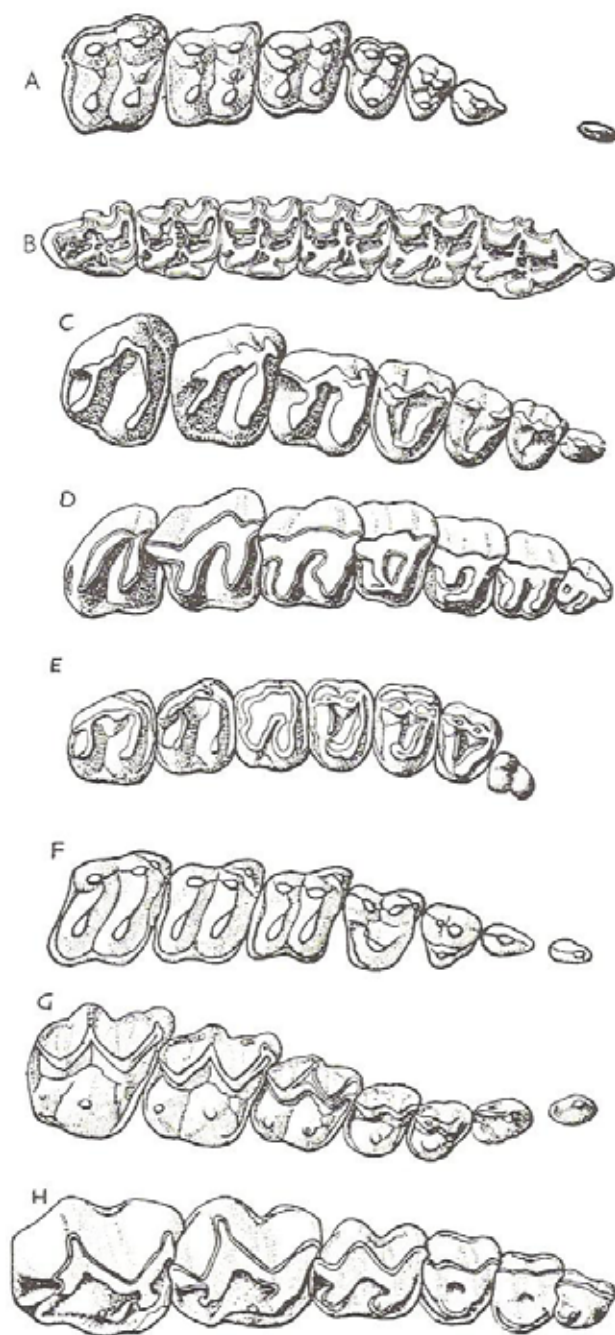


Figure 6. A selection of perissodactyl right upper cheek teeth; after Romer.²⁴ Contrast the top set of teeth from *Hyracotherium* with those below. Relative sizes compared to *Hyracotherium* are given in parentheses. A) *Hyracotherium* (x 1), B) *Equus laurentius* (x 1/2), C) *Hyrachyus* (x 5/3), D) *Subhyracodon* (x 2/5), E) *Protapirus validus* (x 5/9), F) *Homogalax* (a moropomorph, x 1), G) *Palaeosyops* (x 5/12), H) *Moropus* (x 1/3).

crown. The presence of extensive cement on their teeth gave these horses large grinding surfaces composed of hard enamel ridges above softer, lower regions of cement and dentin. These ridges acted like tiny shearing edges to

efficiently chop plant material into small pieces.³ *Parahippus* and subsequent equine genera shared other features too. The muzzle is deeper to accommodate the long teeth and the eyes are shifted further back for better vision. The limbs are extended; the lower arms and shins, as well as the toes, are all longer. The genus *Parahippus* represents a heterogeneous assemblage of forms that spans a gradient (morphocline) of dental and postcranial characters. At one end is *Desmatippus*, and at the other *Merychippus*, the first of the Equinae.

The genus *Merychippus* is extremely difficult to diagnose. Its species intergrade almost imperceptibly with those of *Parahippus* on the one hand and those of *Pliohippus*, *Calippus*, *Nannippus*, *Hipparion*, and *Neohipparion* on the other.²⁹ This continuum from *Desmatippus* and *Parahippus* (both considered anchitheres) to *Merychippus* and other equine genera makes it difficult to separate the browsing horses (Anchitheriinae) from the grazing horses (Equinae).²³ However, the major trend towards high-crowned teeth, hypsodonty, was observed in *Merychippus* (this trend is quite distinct from ‘molarization’). So a hiatus between the browsing horses and the grazing horses might exist, being obscured by the precocious appearance of dental cement in *Parahippus* and by ‘subhypsodont’ specimens of *Merychippus*. If a hiatus does exist, then the Anchitheriinae and Equinae represent separate monophyletic families. However, the presence of intermediate fossil species suggests such a hiatus does not exist. High-crowned teeth and monodactyl limbs did not appear simultaneously in the fossil record. Although all extant equids are monodactyl, only in the more recent equine genera did monodactyl limbs appear. The question remaining is what caused the apparently ‘directed’ morphogenetic adaptations of dentition and limbs?

Ecological successions and adaptive radiations during the Tertiary³⁰

Popular contemporary interpretation of the paleontological finds suggests that during the course of the Tertiary period gradual cooling and drying caused major shifts in the dominant biomes, i.e., ecological succession. The subtropical early Tertiary earth was rapidly recolonized by poorly diversified forests which matured into complex deciduous rainforests.^{11,17,18} The fossil evidence indicates that during this period hyracothere-like animals underwent a major adaptive radiation. However, these conditions did not last, and when cooling and drying began during the middle Eocene the subtropical rainforests were replaced by woodland savanna. These more open forest conditions resulted in dominance of the anchitheres, initiating their own adaptive radiation, and the fading away of the hyracotheres.

With further cooling and drying of the global climate, at the Oligocene-Miocene boundary, the woodland savanna was replaced by a grassland savanna. The anchitheres in turn were superseded by the Equinae, which underwent at least two adaptive radiations of their own: first, tridactyl Hipparionini genera filled North America; then, towards the end of the Miocene as the grassland savanna was replaced by prairie, these were replaced with the predominantly monodactyl Equini genera^{11,18} (see figure 1). Extensive changes in both fauna and flora occurred at this time evidenced by a massive decline in the extremely species-rich browsing communities.^{31,32} This may have triggered or fostered the monodactyl equine radiation.^{18,33}

The adaptive radiations which took place are extremely instructive as examples of speciation processes. Two types of adaptive radiation were observed. When an adaptive zone, a novel biome such as woodland savanna or steppe, appeared then branching speciation (cladogenesis) took place which was associated with an increase in species number.³³ This was followed by replacement speciation, where the number of species remained approximately constant but ‘fitter’ descendant species simply replaced ancestral species. Eventually, stasis was reached where essentially no new speciation occurred. In all mammalian radiations, body size has been a character which displayed great variation. In perissodactyl radiations dental characteristics also underwent adaptive radiations. The hyracotheres displayed modest increases in molarization, which may have resulted from access to expanding browsing potential. Cement appeared in the anchitheres. Hypsodonty emerged in the Equinae.²³

Browsing horses and grazing horses are sometimes treated as two separate kinds, or families, of animals.³⁴ Although a distinct possibility, it is not necessary to classify them in this complex manner. It is more parsimonious to assume animals differing primarily in quantitative traits belong to a single kind, or family. This problem is encountered in a number of families. An early attempt was made to separate small cats and big cats into two clades. Reasons included differences in ability to roar, in feeding posture, and in pupil shape. It was found that these phenotypic features were never entirely characteristic of either clade. Eventually, based on hybridization criteria, it could be demonstrated that all cats belong to a single basic type.³⁵ An attempt was made to separate foxes and other canids. Because no fox-like dogs have been observed and a wolf/fox transition would require complex phenotypic change, it is not unreasonable to assign them to separate kinds. Once again, based on hybridization criteria, it was demonstrated that foxes and dogs belong to the same basic type.³⁶ In both cases, large and small but otherwise ‘phenotypically equivalent’ animals belong to a single genetic group. Genetic mechanisms are well

able to account for significant intergeneric diversification during standard speciation events, as will be discussed in a future article. Such mechanisms are sufficient to explain the quantitative phenotypic differences between browsing and grazing horses. There is no need to place these animals into separate kinds. This situation cannot be compared to the fundamental phenotypic hiatus between horses and hyracotheres indicative of separate kinds, or families.

Ancillary characters permit adaptive radiation within fixed basic types

Rates of equid speciation peaked during the middle Miocene when between 11 and 13 genera existed.^{3,18,33} Changes in dentition continued. Hypsodonty developed in the genus *Merychippus* in the Miocene and continued in the genus *Nannippus* in the Pliocene.³⁷ Crown heights, occlusal measurements, and dental patterns all varied morphogenetically. Crown heights in the Equinae displayed unidirectional increase in height reflecting adaptation to grazing strategies in the developing grasslands.¹⁸ This is because grasses are tough and abrasive, containing grit-like silica-body secretions, phytoliths, in the epidermis so they rapidly wear down teeth. Under certain circumstances high-crowned horse species can revert to browsing.³⁸ Limb structure also displayed great flexibility. Limb lengths—upper limbs, lower limbs and digits—all displayed adaptive change promoting cursoriality and speed, which were of great benefit in open grassland environments. Such changes do not require extensive morphogenetic reprogramming. Such ‘ancillary’ character changes are common in many mammalian radiations: dentition in the felids, tusk morphology in the Proboscidea, horn structure in the Antilocapridae and Dromomerycidae, etc. Such ancillary character variation does not alter the basic type of animals but it generates important adaptive variation and can be readily programmed into a genome.

Another adaptation, the transition from tridactyly to monodactyly, was not unique to horses. Several families of ungulates lost toes, though few did so to the extent observed in the monodactyl equids. A notable imitation, however, is to be found among the horse-like but unrelated litopterns, a group of extinct herbivorous South American ungulates. The monodactyl *Thoatherium* appears to be descended from the tridactyl *Diadiaphorus*, mirroring this morphogenetic change observed in the Equinae.³⁹ This transition took place during the early Miocene, which was sooner than the equid transition, probably because grasslands became established sooner in South America.¹⁸ Interestingly, *Thoatherium* had low-crowned browsing teeth; it had developed one-toed feet without becoming a grazer. In the legs of another group, the ruminant artiodactyls, which include cattle, deer, and

antelopes, the loss of lateral metapodials and fusion of central metapodials (forming the cannon bone) are skeletal adaptations functionally similar to the adaptations in horses, and both types of adaptation enhanced sustained running capabilities.¹¹ Here too, ancillary adaptation is a phenomenon associated with speciation in various mammalian families. Ancillary adaptations do not alter the type of organism, are easily accounted for morphogenetically, and endow a group with great adaptive variation.

Within the Equidae, other variable characters include cranial elongation (preorbital muzzle length) and incisor morphology patterns. In addition to a simple lengthening of the preorbital region, the skull underwent many other biomechanical changes that are interpreted as adaptations to grazing. Radinsky^{40,41} observed that such changes were not gradual. Instead they occur sporadically when novel adaptive zones appear, e.g. during the transition from *Miohippus* to *Merychippus*, primarily within *Parahippus*. Simpson⁴² introduced the following terms: brachytely, for static taxa (e.g. coelacanth, ginko); horotely, for ‘normally’ changing taxa; and tachytely, for rapidly changing taxa, particularly those invading novel adaptive zones. Clearly, *Parahippus* and *Merychippus* were tachytelic genera. Besides climate and vegetation, other factors would also have promoted the adaptive radiations observed in these genera: factors such as changing predator-prey relations, which would affect limb length to increase speed, and coarseness of soil particles ingested when grazing on short or sparse grasses, which would affect dentition.^{3,18}

Conclusions

Based on morphological criteria, it seems reasonable to include the Hyracotheriinae and various other contemporary and related genera into a monophyletic group. Besides the hyracotheres, the group includes *Radinskya*, various generalized morpomorph families, various species conventionally believed to be primitive brontotheres and chalicotheres, and probably the palaeotheres (see accompanying article). Together these species form a family or created kind. The members of this clade apparently underwent a major adaptive radiation during the early Eocene when subtropical deciduous rainforests were the dominant global biome. Subsequent fragmentation of the group due to climatic and oceanic conditions (vicariance events) would provide an explanation for differences observed between the closely related North American hyracothere-like perissodactyls and the European palaeotheres.

There is evidence of descent with modification in the adaptive radiations of the Tertiary horses, as a family independent of the Hyracotheriinae. Horses got larger, their

teeth longer, and their toes fewer. Descent with modification is thought to have occurred in other families too. Rather than being a completely stochastic process, it appears that adaptations have been directed by climactic change and resultant biome change, i.e. ecological succession. As novel adaptive zones arise, they bias the direction of the adaptations of the animal species present. These species in turn can influence the development or establishment of the existing biomes. Adaptive radiations of the horse give well-documented and reasonably complete histories of the impact of these changes on ungulate habitats. They provide a pattern with which to compare, and from which to extrapolate, aspects of the adaptive radiations of other more poorly documented fossil groups.

An important observation is the prominent contribution of plastic ancillary characters during adaptive radiations. The morphological changes in the phylogeny of horse species were affected by ancillary adaptations. Such adaptations can be explained as the result of modest morphogenetic reprogramming. A continuum of speciation events led to the establishment of various novel horse genera. However, there is no convincing evidence to suggest that horses were either derived from another type of organism or changed their basic type to become another sort of organism. The proposed transition from early tapir-like hyracothere to Oligocene browsing horse remains specious argumentation at best.

In 1940, Stirton³⁷ proposed a very realistic phylogeny (although *Dinohippus* rather than *Pliohippus* is now considered the closest outgroup of *Equus*¹⁸). He indicated a clear hiatus at the *Epihippus*-*Mesohippus* boundary and specifically writes into his phylogeny: “Intergradation between *Epihippus* and *Mesohippus* not proved.”³⁷ This is still true. The hyracotheres had at best only partially molarized premolars. Their limbs were less restricted in their movement, causing a looser gait, which is far removed from the typical springy, yet precise, leg movement of horses. There is evidence that the functional digits of the tetradactyl manus and the tridactyl pes terminated in pads. In contrast to horses, hyracotheres probably lacked bony hooves.^{3,43} In terms of overall locomotion, the hyracotheres had a less springy gait and lower maximum speed.⁴³ The hyracotheres also demonstrated a different stance with less-elevated shoulders when compared to horses. Given that extant tapirs are generalized for these features (but not the specialized skull and proboscis) they serve as a “close functional analogue”³ for these early generalized perissodactyls. Thus, hyracotheres were small, morpomorph-like animals. Till the present day Stirton’s observation holds: “Intergradation between *Epihippus* and *Mesohippus* not proved.”³⁷ Ernst Mayr acknowledged Stirton’s gap in his seminal book *Principles of Systematic Zoology*. He commented: “It is true that the fossil record gives substance to phylogenetic

trees, but the gaps in the record are still sufficiently large even in the best-known groups to require much conjecture.”⁴⁴ Franzen affirms this stating: “The continual transition from lower Eocene *Hyracotherium* to middle Eocene *Orohippus* as well as from *Orohippus* to *Mesohippus* has still to be substantiated by fossil evidence.”⁴⁵

Franzen, a leading European authority on horse evolution, in his recently translated reference book *The Rise of Horses* writes, “We are still a long way from tracing evolutionary development of the horse from species to species. Considering the gaps in the fossil record, it is questionable whether we will ever achieve this aim.”⁴⁶ He is the world expert on three European, hyracothere-like genera: *Propalaeotherium*, *Hallensia* and *Eurohippus*; whose remains, even soft body parts, were wonderfully preserved at various sites in Germany, including Grube Messel, and which are considered a side branch of the equid line that went extinct. These ‘dawn-horse’ genera are all similar, and belong to the stem group *Hyracotherium*, though more primitive (i.e. less horse-like). Small as a fox terrier, possibly loping along like a rabbit, and with an arched back like a duiker or muntjac; in response to the question, how could this small animal, *Hyracotherium*, arrive at its position as the ancestor of all horses, Franzen candidly acknowledges the importance of “theoretical considerations”⁴⁶ (i.e. interpretive bias) play in such deliberations. In addition, in response to the anterior question, how such animals could have evolved from an ancestral dawn-ungulate Franzen concedes, “The first chapter in the evolution of the horse—during which all of these developments took place—is missing.”⁴⁶

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