The Geological History
and
Evolution of the Horse

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GEOLOGY
LEAFLET 13

FIELD MUSEUM OF NATURAL HISTORY
CHICAGO, U. S. A.
1932

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GROUP OF THREE-TOED HORSES IN FIELD MUSEUM

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FIELD MUSEUM OF NATURAL HISTORY
DEPARTMENT OF GEOLOGY
CHICAGO, 1932

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THE GEOLOGICAL HISTORY AND EVOLUTION OF THE HORSE

INTRODUCTION

The horse family is made up of a large and varied group of animals. It includes the true horses of several domestic breeds, a single species of wild horse, and various species of wild asses and zebras. All of these are modern animals, now living in various parts of the world. In addition there are included in this family many kinds of extinct horses which have lived at various periods of the earth's history.

The horse family furnishes one of the best-known examples of evolution. This is due to two important factors: First, the horse has, during his history, undergone great changes both in size and in structure; second, the records have been so well preserved that almost every important chapter in the family history, during a period of millions of years, is known and recorded. This makes possible a detailed study of the evolution of this animal.

While the domestic horse has long been known to men of all countries, the wild horse is known only from a single species which lives in isolated parts of Asia. Other species were known to prehistoric man and were recorded by him in carvings and paintings on the walls of his cave dwellings. Still others are known from bones which were accumulated about the rock-shelter habitations, as primitive men feasted upon the animals and threw their bones into refuse heaps.

The more ancient species are known only from the bones and skeletons which are found buried in the earth as fossils. Such remains are preserved by natural agencies. They furnish evidence of by far the larger number of species of extinct horses. This evidence makes possible the study of many extinct members of the horse family which would not otherwise be known to science. By such study the history of the horse has been traced through five geological periods from remote times down to the present.

Studies in the evolution of the horse are largely based upon comparisons of the fossil animals of one period with those of another. Variation of structure in mouth-parts and in foot, and a general increase in size are usually observed. These variations are followed through the animals of successive periods until a general trend of changes is discovered. Following through the entire history of the horse family, these changes become very great.

Changes in the bony structure of the horse are in some instances traceable to, or correlated with, changes in habits of the animal. Sometimes a direct relation between structural variations of the animal and general changes of climate or of food materials may be recognized. In this way causes of structural changes may be discovered.

The evolution of the horse has been complicated by continuous branching of the family into new and different directions. Some of the branches continued only a little while in comparison with the life of the family as a whole. Others continued for longer periods, extended their range over large sections of the earth and became well established. The main line gave rise to the modern horse; other branches which have continued until modern times are represented by the zebras and the asses.

MODERN HORSES

THEIR DISTRIBUTION AND USE

The horse is one of the best known of all domestic animals. He has served as a mount and as a beast of burden in almost all civilized countries. Among barbaric peoples the horse has been known and prized. As the companion and the servant of man he has found his way into all continents and into remote islands wherever human habitation is possible. When introduced into North America by the Spaniards, the horse soon became distributed through the wide plains of the interior where the natives had known no larger domestic animal than the dog. In the same way the horse became known to the pampas of South America as far as the Straits of Magellan. In both continents horses readily adapted themselves to the new home and in many places ran wild in large numbers.

The time and place of the first domestication of the horse are lost in the shadows of antiquity. Probably it was domesticated in many localities and from as many as two or three species. The domestic horses of western Europe and of America have come from an admixture of at least three different stocks. The sturdy and long-haired Celtic horse, known to men of the later stone age in Europe and painted and carved upon the walls of their caves, apparently furnished the bone and sinew from which the larger breeds have been developed. Horses of this type were in common use among the Gauls, the Britons and the Germans at the time of the Roman invasion of western Europe.[1] An African breed of horses of taller stature and more slender build is known to have been brought into Europe by Hannibal's troops, and later an animal similar to the modern Barbary horse was imported from Africa by the Gallic chieftains to furnish them with

[1] William Ridgeway, The Origin and Influence of the Thoroughbred Horse, 1905.

swifter mounts in their struggle with the Romans. These animals have doubtless furnished the more agile stock from which have developed the fleet-footed breeds. The gray Arab horse, brought back to Europe by the Crusaders, also added his influence to our modern domestic stock.

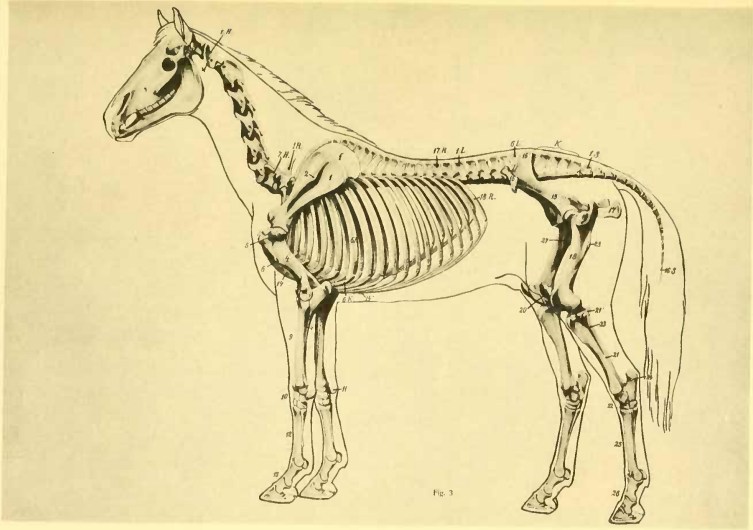
THE BONY STRUCTURE OF THE HORSE

In order to make clear the study and comparison of the different members of the horse family, let us first examine the important features in the bony structure of the modern horse (Plate II).

The horse is a four-footed animal which walks upon single, rounded hoofs and in his wild state feeds chiefly upon grass. His long neck enables him to reach up and crop leaves from trees and bushes and to reach the ground in feeding or drinking. His legs are rather long and are freely movable in a backward and forward direction only. The muscles of his legs are placed near his body and are connected with the movable parts by long tendons so as to give the great freedom of motion required in a swift-footed animal. His firm hoof at the end of a flexible foot gives him a secure footing upon all kinds of ground. From his records as a racing animal he is justly considered as one of the swiftest of all running animals.

The skull (Plate III, fig. 1).—It will be observed from the skull that the face of the horse is very long. The eyes are far back from the nose and they are entirely enclosed by a bony ring (orbit). The arch back of the eye is very short, and the braincase is short and rounded. The base of the braincase forms a decided angle with the long axis of the face. A sharp ridge (masseteric ridge), not found in the skulls of other animals, extends forward from below the eye, along the side of the upper jaw. It forms an extended anchorage for the muscles which attach to the lower jaw.

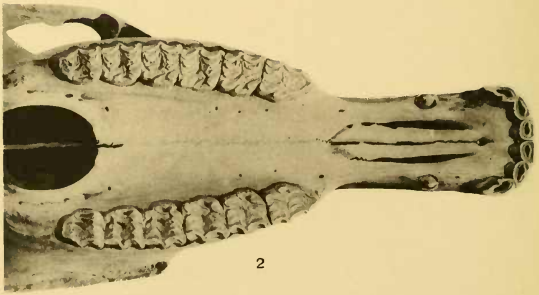
The teeth (Plate III, figs. 2, 3).—The horse has, above and below, three pairs of front teeth called incisors. These



SKELETON OF MODERN HORSE

1H–7H. Cervical vertebrae. 1R–17R. Dorsal vertebrae. 1L–6L. Lumbar vertebrae. K. Sacral vertebrae. 1S–16S. Caudal vertebrae. 6R–18R. Ribs. 6K. Costal cartilages. 1. Scapula. 2. Spine of scapula. 4. Humerus. 5. Tuberosity of humerus. 6. Deltoid crest. 7. Ulna. 8. Olecranon. 9. Radius. 10. Carpal bones. 11. Unciform bone. 12. Metacarpal bones. 13. Phalanges. 14–14″. Sternum. 15. Ilium. 16. Crest of ilium. 17. Ischium. 18. Femur. 19. Great trochanter. 20. Patella. 21–21′. Tibia. 22. Tarsal bones. 23. Fibula. 24. Calcaneum. 25. Tarsal bones. 26. Phalanges. 27. Second trochanter. 28. Third trochanter.

1



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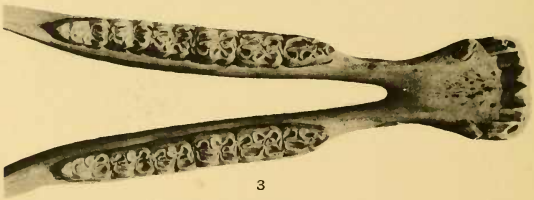

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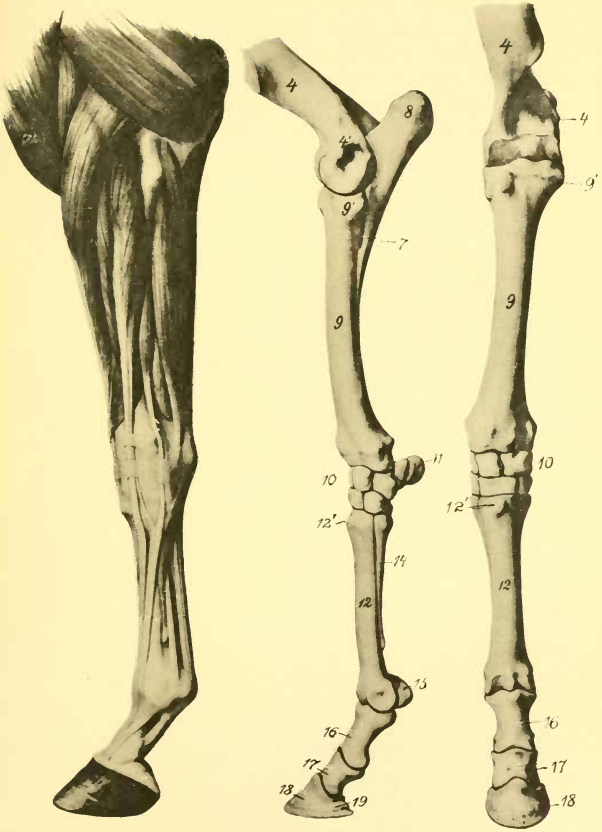
SKULL AND TEETH OF MODERN HORSE

teeth wear smooth at the crown and meet closely so as to enable him to seize small blades of grass and to bite them off close to the ground. They are preceded in the young animal by an equal number of milk teeth. Behind the front teeth is a wide space known as the bridle-gap or diastema. In this gap often appears, in the full-grown animal, especially in the male, a rounded fang or canine tooth known to horsemen as the wolf tooth. In some horses, but rarely, a second rounded tooth appears farther back in the bridle-gap. Back of the bridle-gap there are six pairs of grinding teeth both above and below. The first three pairs are preceded by milk teeth and are called premolars. The last three pairs of teeth appear during the later growing stage of the animal and are called molar teeth.

The legs and feet (Plates IV, V).—While both fore and hind legs are attached to the body by ball and socket joints, they are controlled by muscles which do not admit of a rotary movement. Each leg is composed of three sections which may be called upper, middle and lower. The bone of the upper section of the fore leg (humerus) is proportionately short, that of the middle section (ulna-radius) one-fourth longer, and that of the lower section (metacarpal) somewhat shorter than that of the upper section. The various bones join each other in hinge joints. The upper section of the hind leg is slightly longer than the middle and lower sections; all are attached by hinge joints. The construction of the knee is quite different from that of the elbow joint, though both have a similar movement.

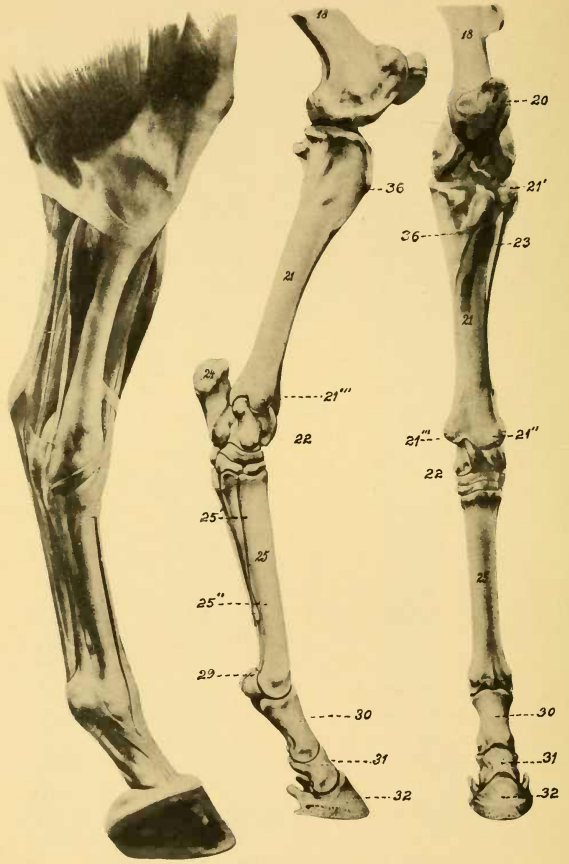
The two bones of the middle section of the fore leg are joined together in one piece. The smaller bone of the middle section of the hind leg (fibula) is represented by a small bony knob at the lower end of the larger bone. The bones of the lower section of both fore and hind leg consist of a strong, rounded bone, called the cannon bone (third metacarpal or metatarsal), which supports the

weight of the animal, and of two flattened bones (splints) which lie closely on either side of the cannon bone. The splint bones usually extend no more than two-thirds of the way to the fetlock joint. Their upper ends are larger and form part of the movable joint; their lower ends terminate in small rounded knobs without attachment of any kind. Below the fetlock joint there are three short bones (phalanges) which correspond to the three joints in a human finger or toe and which constitute the skeleton of the horse's foot. The last of these three bones (the ungual) bears the enlarged hoof which corresponds to the nail on the human finger or to the claw of a dog. The foot of the horse is, in fact, an enlarged third toe and corresponds to the third finger of the human hand.



FORE LEG AND FOOT OF MODERN HORSE

4. Humerus. 7, 8. Ulna. 9. Radius. 10, 11. Carpal bones. 12, 12′. Third metacarpal. 14. Fourth metacarpal. 15. Sesamoid bone. 16. First phalange. 17. Second phalange. 18. Third phalange.



HIND LEG AND FOOT OF MODERN HORSE

18. Femur. 20. Patella. 21. Tibia. 21′. Fibula. 22. Astragalus. 23. Fibula. 25. Third metatarsal. 25′. Fourth metatarsal. 25″. Second metatarsal. 29. Sesamoid. 30. First phalange. 31. Second phalange. 32. Third phalange. 36. Spine of tibia.

THE GEOLOGICAL HISTORY OF THE HORSE

Evidences of the horse as a prehistoric animal are partly derived from the carvings and picture-writings made by primitive man, and from the bones of horses found in and about their habitations. A larger fund of evidence has been derived from the fossil remains of ancient horses which have been preserved in the earth by nature. Such remains are found in clays, in sands, and in harder rocks of varying age.

It is at once observed that the bones of fossil horses which belong to the later geological periods are quite similar to those of the modern animal. Those of older formations are found to be more and more widely different. The oldest horse ancestors could not be recognized as such until intermediate links had been discovered and closer comparisons were thus made possible.

The bones of some later species of fossil horses are as large as the bones of the ordinary stock of wild horses now living. Their heads are similar in form and in proportions to those of modern horses. Their eye sockets and their nostrils are in similar positions. They have the same number of teeth, and teeth of the same form and appearance as those of our modern horses. We naturally infer that the two are nearly related.

Remains of such fossil horses are found in the clays which underlie the soil in river valleys of many localities and in the drifted sands of Nebraska and of Texas. They are of Pleistocene age. The fossil bones of horses found in older rock ledges such as the semi-hardened sandstones (Plate VI, fig. 1) of Kansas, Nebraska and the Dakotas, have a different appearance. The bones are more stained and colored, they are heavier, and in most instances are partly petrified, or "turned to stone."[1] The skulls are smaller, the jaws more slender, the nose tapering and the

[1] Petrifaction is a slow process of replacing animal matter by mineral.

teeth shorter. The leg bones are shorter, the hoof bones are smaller and more pointed, and a second and a third hoof are found on each side of the principal hoof, connected by the toe bones to a flat bone on either side of the leg which corresponds to the splint in the modern horse. These are the "three-toed" horses. That is, the feet of these animals were provided with three hoofs instead of one, and each hoof with its connecting joints formed a separate toe. These horses belong to the Miocene period.

In the hardened clays of the "bad lands" of the Dakotas, of Nebraska, Wyoming and Colorado (Plate VI, fig. 2) are found the bones of little, horse-like animals, barely one-third the height of a modern horse and proportionately small and slender (Plate VII). The short face, tapering to a small muzzle, and the shorter and smaller teeth with fewer grinding ridges on the crowns of the molars, remind us less of the horse than do the larger three-toed animals described above. Also the neck is not so long and the hoofs are smaller, the middle hoof being no more than twice as large as those on each side of it. These are the earlier three-toed horses of the Oligocene period—animals not larger than a collie dog (Plate X, figs. 1, 2).

If we search long and carefully among the hardened clays and sandstones in the various "bad lands" of western Wyoming, of Utah and of New Mexico, we may find, rarely, the bones of a little animal no larger than a fox (Plate VIII). In this animal the head is narrow with a pointed nose, the jaw is slender, the teeth short and simple in pattern. The neck and legs are short, the back rounded in profile. The fore feet bear four small hoofs of almost equal size and the hind feet three hoofs. These are the "four-toed" horses, the smallest members of the horse family known to North America. Two skulls of a slightly more primitive animal have been found in southern England. These little horses lived in the Eocene period.

In general it is observed that as we go backward in the geological scale, dealing with older and still older periods, the fossil horses become more and more unlike the modern horse. As a rule they become successively smaller, more primitive in their structure, and fitted for different habits of living.

These observations, followed by careful and painstaking study by many scientists, have led to the conclusion that the horses, as we now know them, are descended from this small, four-toed ancestor. It has been observed that during long ages the descendants of this animal have grown larger; have increased in the proportionate length of their neck and legs; that their teeth have changed from those of a simple pattern to one more complex; and that one by one they have lost the three side toes, while the central toe grew large and strong so as to support the animal on a single hoof.

This is the process we shall presently examine in detail, a process of slow change in size, in structure and in habits, from parent to offspring, through forty-five million years —the evolution of the horse.

HOW THE REMAINS OF EXTINCT ANIMALS ARE PRESERVED

The study of fossil animals is based upon the hard parts of their bodies, which are preserved in the earth and in most cases petrified. The skin and the flesh are never petrified; in a few instances they have been preserved as natural mummies. Therefore, in studying the remains of extinct horses, we have to rely upon the bones and the teeth for our knowledge of the animals. These hard parts furnish us with greater evidence than at first might be supposed. The skeleton not only gives evidence of the size and the proportions of the animal, but preserves each point of attachment for muscle, tendon or ligament. The attachments show what muscles of the body were developed, and to what extent such muscles were used. This in turn gives a clue to the habits of

movement, showing whether the animals were runners, jumpers, climbers or swimmers. The formation of the foot also gives evidence of the animal's movements and of the kind of lands he inhabited. The structure of the teeth and the wear to which they have been subjected, tell us much of the kind of food which was consumed by the animal.

The teeth and bones of fossil animals are sometimes preserved in peat bogs and in swampy lands. In such places they may be preserved for long periods of time by the natural tanning action of the vegetable acids produced by the decay of plants. The bones may be preserved also in beds of clay, sand or gravel without any noticeable change in their form or structure, but such bones will, in most instances, have become very brittle and may fall to powder when long exposed to air. Bones may be preserved for much longer periods of time by being petrified, becoming stone. Most of the remains of extinct horses available for study are petrified. Such objects are collected and preserved in museums of natural history for the purposes of study and of exhibition to the public. Many splendid skulls of extinct horses and a smaller number of entire skeletons are preserved in the museums of this country and of the entire world.

HISTORICAL ACCOUNT OF THE EARLIER FOSSIL HORSES

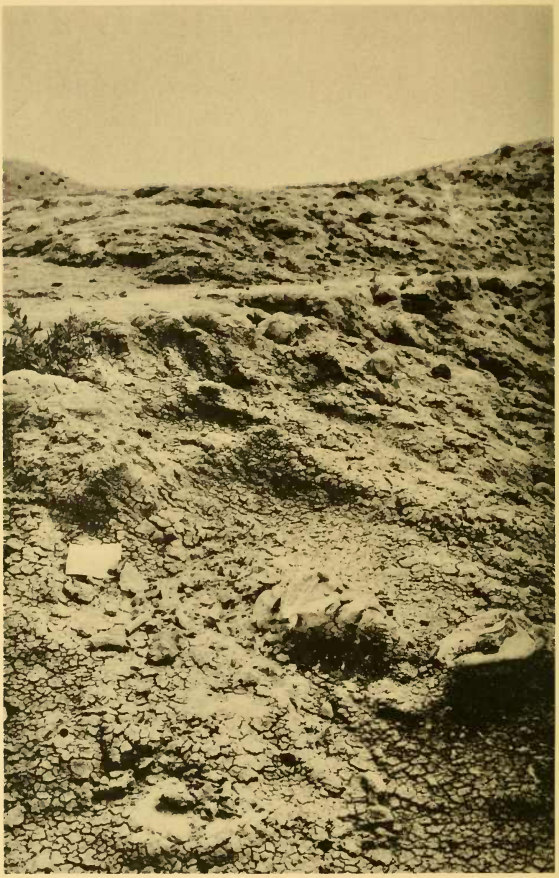
EOHIPPUS, LOWER EOCENE PERIOD

The scientific names of extinct horses are derived from a Greek word, *hippus*, which signifies "horse." Before this word is placed an adjective which points out some particular characteristic of the animal to be named. In this way the earliest known horse in America has been named *Eohippus*. This name signifies the "dawn horse."

Eohippus (Plates VIII, IX) was no larger than a fox. It stood only eleven inches in height at the shoulders. The neck was short, the body was plump and rounded. The legs were adapted to running habits and perhaps were

1. LOWER MIOCENE FORMATION, PINE RIDGE, NEBRASKA
Photograph by author

2. OLIGOCENE "BAD LANDS," SOUTH DAKOTA
Photograph by S. W. Williston



FOSSIL SKELETON OF THREE-TOED HORSE, *Mesohippus bairdii*, "BAD LANDS," SOUTH DAKOTA

Photograph by author

DISTRIBUTION OF HORSES THROUGH GEOLOGICAL PERIODS†

Name of period	Age of period	Genus of horse present
Recent	Modern times	*Equus,** true horse
Pleistocene	1,000,000 years	*Equus,** true horse
Pliocene	7,000,000 years	*Plesippus,** one-toed horse *Hipparion*, three-toed horse *Hypohippus*, lowland three-toed horse *Pliohippus,** latest three-toed horse
Miocene	19,000,000 years	*Pliohippus,** latest three-toed horse *Hypohippus* *Merychippus,** later three-toed horse *Anchitherium*, forest horse *Parahippus,** three-toed upland horse
Oligocene	35,000,000 years	*Miohippus,** three-toed horse *Mesohippus,** first three-toed horse
Eocene	50,000,000 years	*Epihippus*, four-toed horse *Orohippus,** four-toed horse *Eohippus,** four-toed horse
Paleocene		No known horse

†Successive periods in geological history are represented on the diagram above by divisions which correspond to successive layers of rocks in the earth which were formed during consecutive periods.

Of these rock layers the upper ones were formed last and are newest, the deeper-lying layers are older. Thus, as we pass downward in the scale, we come to older and still older rocks. A number of layers grouped together are designated as a geological formation. The time allotted to accumulating such a formation is designated as a geological period.

In this way we have, as here shown, a series of geological periods. With each period is given an estimate of its age, based upon calculations by the late Professor Barrell, which are generally accepted by geologists as reliable. In the several geological periods is indicated the kind of horse whose remains are found buried in the rocks of that period. In this series we find in the Lower Eocene period animals very unlike the horse. In the successive periods above are found horse-like animals which approach nearer and nearer to the true horse. In the Pleistocene period are found fossil animals recognized as true horses. In the Recent period is found the modern horse.

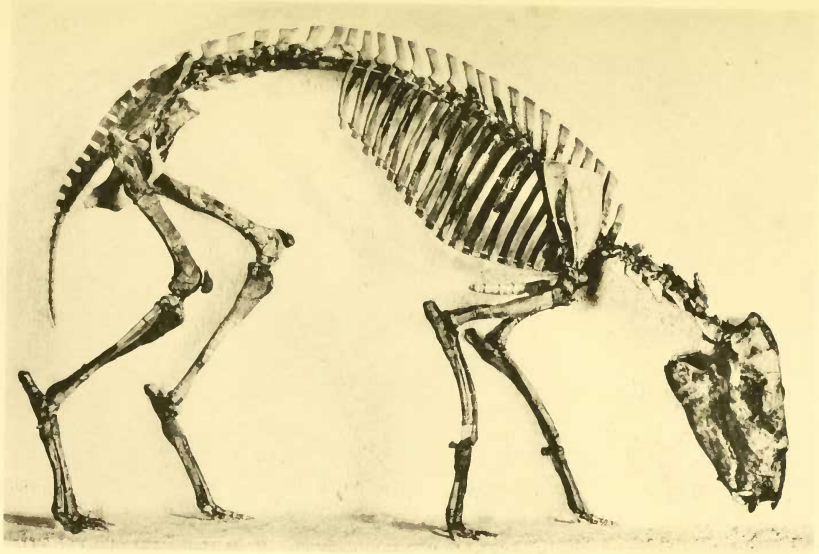
*In direct line of descent.

as nearly like those of a fox as of any well-known animal. The feet had four toes in front and three toes behind. In addition there were vestiges of two additional toes in the hind foot.[1] All the functional toes ended in narrow, tapering hoofs, of which the middle one was slightly longer than the others. The animal walked upon a pad at the base of the toes very much as a dog or a fox walks. The hoofs were pressed against the ground in the act of stepping and served to grip it more firmly, as do the human toes, but they bore little of the animal's weight (Plate VIII). The teeth were simple in structure and adapted to feeding upon leaves and soft, fleshy plants.

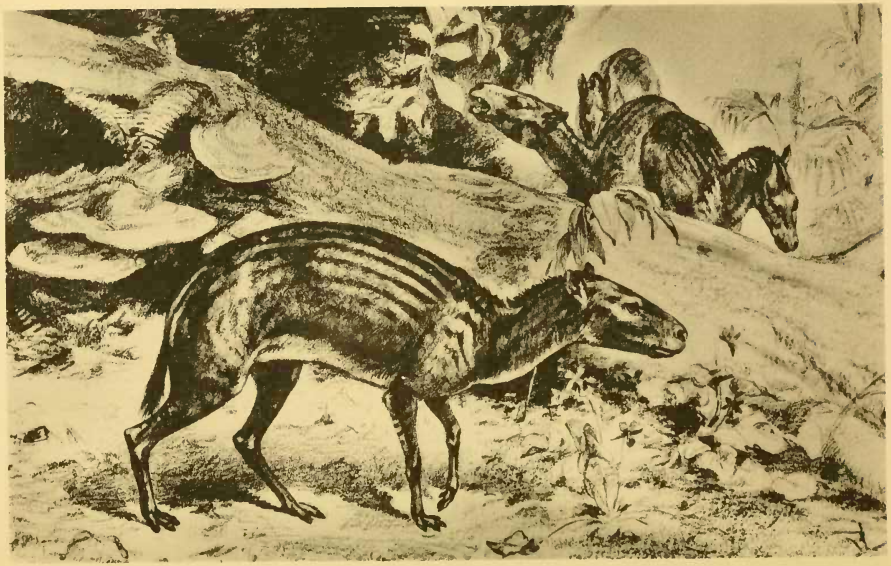
While *Eohippus* may have lived in small herds, as wild horses of modern times do, it is not probable that these animals could have relied entirely upon their swift-footedness to escape the larger flesh-eaters which preyed upon them. They must rather have found protection in concealment among bushes and other vegetation. Having strong hind legs and a stout back, these animals were equally well qualified as leapers or as runners. By alertness and quick movement they doubtless found means of eluding their natural enemies, though often a lagging member of the troop was seized by a flesh-eater which lay in wait for him.

These little ancestors of the horse are known to have lived along the eastern slope of the Rocky Mountains. They were probably distributed over a large part of North America, but of the exact extent of their range we have no evidence. Their fossil remains have been found in various "bad land" areas of Wyoming and of New Mexico. In these localities the bones of *Eohippus* have been petrified and so preserved. Though darkly stained with iron and other minerals of the earth, the fossil bones and teeth

[1] As the primary number of digits, or toes, in the feet of mammals is five, the toes are numbered one to five, beginning with the inner one and numbering outward. In those horses which have lost the first toe, the innermost toe is designated as second, the outer as fifth. In the modern horse, the remaining toe is the third.



SKELETON OF FOUR-TOED HORSE, *Eohippus resartus*
Photograph by American Museum of Natural History



RESTORATION OF FOUR-TOED HORSE, *Eohippus resartus*
By Bruce Horsefall

retain nearly all the markings of such parts in modern animals. Excellent examples of skulls and jaws with teeth, and in a few instances entire skeletons, have been found.

The first discovery of *Eohippus* was made known by Professor O. C. Marsh of Yale University in 1876. The first entire skeleton of this animal was discovered and described by Professor E. D. Cope of Philadelphia in 1885. This rare specimen is preserved, with a second found in 1911, at the American Museum of Natural History, New York (Plate VIII). Other specimens may be seen in various museums of America.

These fossil skeletons bear unmistakable evidence of the size and characteristics of *Eohippus*. Two skulls of similar animals (*Hyracotherium*) have been found in the vicinity of London. They are preserved, one in the Museum of Natural History at South Kensington and the other in the Royal College of Surgeons, London. The presence of these specimens leads to the conclusion that animals similar to *Eohippus* lived in the region now known as the British Isles about the same time that *Eohippus* lived in western North America. There is reason to suppose that similar animals may also have lived in parts of Asia.

When *Eohippus* lived in North America the climate was more uniform and milder than at the present time. Rainfall was then much greater on the eastern slopes of the Rocky Mountains and vegetation in many localities is known to have been abundant.[1] The Rocky Mountains were then a newly formed range with their bases but little elevated above the sea level. The Sierras had not yet risen to cut off the moisture-laden winds from the Pacific.[2] The abundant rainfall on the eastern slope

[1] On the subject of geological climates, F. H. Knowlton, late paleobotanist of the United States Geological Survey, has adduced much evidence derived from the study of fossil plants of various localities, which indicates that climate in North America during the Eocene period varied from warm temperate to sub-tropical. Bull. Geol. Soc. Amer., **30**, pp. 528–532.

[2] J. Le Conte, Jour. Geol., **12**, pp. 528–530.

of the Rocky Mountains was carried by numerous streams down into the mountain basins and far out upon the low-lying plains. Copious vegetation, such as is now common to the Gulf States, and large forest trees of many species are known to have been common in various localities during the earlier part of the Eocene period.[1] Among such surroundings the little *Eohippus* lived, along with other animals of his time, in the mountain basins of Wyoming and New Mexico.

The rivers which flowed down from the mountains carried with them as is common, especially in time of flood, a burden of clay sediments and of fine sand. When they overflowed their banks these materials settled in the more quiet backwaters and there accumulated from year to year. Animals which lived about the streams left their remains to be covered over by these sediments. Others were mired in quicksands or left their skeletons to accumulate about the drinking places just as sheep and cattle now do. Ages afterward, when the base of the Rocky Mountains was raised higher and the Great Plains were elevated, streams ran more swiftly out of the mountain basins. Then the streams cut their channels more deeply through the accumulated layers of old sediments. In time the basins were cut and furrowed by new stream channels and in this process the fossil skeletons were laid bare. In this way evidence of animals of that far-off time has been revealed.

OROHIPPUS, MIDDLE EOCENE PERIOD

In the Middle Eocene formations of the Bridger Basin, southwestern Wyoming, are found various other fossil horses. They lived some millions of years later than the *Eohippus*. One species is known from an entire skeleton, another from a skull and a fore foot, others from fragments of jaws with teeth. From these specimens, which vary among themselves in minor details, a number of different

[1] Knowlton, *loc. cit.*

species have been named. All are included in a group (genus) under the name *Orohippus*, the "shore horse."

The horses of this time were somewhat larger than the *Eohippus*, but in general proportions they were quite similar. If we examine closely the teeth of a specimen of *Orohippus* we shall find that it differs from those of the earlier horse in certain definite particulars (Plate XVIII, fig. 2). The fourth upper premolar tooth has a four-sided crown instead of the three-sided crown in the same tooth of the earlier horse (Plate XVIII, fig. 1). Also, there are two cone-shaped cusps on the inner half of the crown in place of the one simple cone in that of the earlier animal. In short, this tooth has taken on the form and the crown-pattern of the molar teeth, and is actually larger than the molar teeth. This animal, therefore, has four crushing teeth instead of three, as in *Eohippus*. In addition to this change, the third premolar tooth is noticeably larger than the corresponding tooth in the earlier horse. The feet of this animal have the middle toe slightly stronger than that of *Eohippus* and the hind foot has lost the vestige of an outer (fifth) toe.

These may at first appear to be small differences, but by such changes in structure the evolutionary development of the horse may be followed.

EPIHIPPUS, UPPER EOCENE PERIOD

In the Upper Eocene formation of the Washakie Basin of southern Wyoming, there have been found the fossil remains of another early horse known as *Epihippus*. This animal was somewhat removed from the main line of horses, so he has been given a name which signifies the "animal-beside-the-horse." These horses are not so well known as the last two described. Only two species have been included under this name, and no entire skeleton of either has been found. The major differences between this animal and *Orohippus* are along the same line as those pointed out between the first two kinds of horses.

The third upper premolar tooth, grown larger in *Orohippus*, has in *Epihippus* (Plate XVIII, fig. 3) reached the size and taken on the pattern of the molar teeth. The horse is now equipped with five effective crushing teeth instead of the original three. If we look further we find that the second premolar tooth of this animal has four cusps instead of the three in the earlier horse, and that the crowns of the molar teeth stand higher than in *Orohippus*. These features are forecasts of further developments in tooth structure. In the feet, the middle toe is stronger than in either of the earlier horses and the outer or fifth toe of the fore foot is weaker, though still of service to the animal.

As has been said, *Epihippus* is not regarded as in direct line of descent of the later horses, but rather as a conservative side branch which did not give rise to the horses of the next period. The direct ancestor of *Mesohippus*, according to Professor W. D. Matthew, should be a more progressive animal which perhaps inhabited the more northerly part of North America. It is to be hoped that the continued search which has been carried on for a number of years in the Upper Eocene formations will bring to light specimens which will more nearly connect the line of descent from *Orohippus* to the Oligocene horses.

MESOHIPPUS AND OTHER HORSES OF THE OLIGOCENE PERIOD

The horses of the Oligocene period in North America are better known than those of any previous stage of horse history. This knowledge is due to the excellent preservation of their fossil remains and to conditions which have made them easily recovered for purposes of study. These favorable conditions are found in the famous White River "bad lands" of South Dakota and adjacent states (Plate VI, fig. 2).

The sediments which were washed down by streams from the Black Hills, and from the Rocky Mountains farther westward, millions of years ago, accumulated on

the level plains to a depth of four hundred feet. The remains of animals living there were covered over and preserved in these layers of clays and fine sand, much as the remains of *Eohippus* had been preserved in the mountain basins of northern Wyoming, but more perfectly. The abundance of fossil remains shows that species of horses had lived there in large numbers.

In the course of time the action of streams was reversed. They began to wear away the plain. The streams which flow eastward from the elevated lands about the Black Hills have in later times cut their valleys through this plain. In turn, their tributaries of larger and smaller size have cut and furrowed the yielding clays which lay below the surface until large areas are laid bare in the ridged and guttered shapes which are called "bad lands."

Remains of animals washed out of the earth in this process of erosion are readily discovered. The large areas of clays exposed as collecting grounds, and the beautiful preservation of the fossil teeth and bones found in them, have made this formation the Mecca of all collectors. Among the remains of two hundred species of fossil animals which have been found in this formation, are those of two distinct kinds of horses. Specimens of these horses are preserved in many museums throughout the world. They include a number of entire skeletons as well as many skulls, jaws, feet and other parts of skeletons.

Of these two kinds of Oligocene horses no less than thirty species have been recorded from North America. The different species do not show such great variations as might be expected from so large a number. The horses of the earlier and middle divisions of the period are included in the group named *Mesohippus*. This name signifies "middle horse," a term so given to indicate that this animal was midway in the horse development—midway from the earliest known species to the modern horse. The horses of the later division of the Oligocene period are classified under the name *Miohippus*. The most com-

mon of all the species of this period, and one known from several splendid skeletons, is called *Mesohippus bairdii*. The name translated into English means "Baird's middle horse." This species will be taken as a typical representative of the Oligocene horses (Plate X, figs. 1, 2).

Animals of this species reached a height of twenty-four inches at the shoulders. They were about as large as a collie dog, but were more slender. The head was narrow and tapered to a pointed nose. The neck was rather short and the back rounded upward from shoulders to hips. The legs were slender, the feet had three toes, fore and hind, and all bore hoofs. This was the first of the three-toed horses.

Compared with *Epihippus* of the later Eocene period, we find that *Mesohippus* showed some marked differences. These were: (1) A considerable increase in size; (2) the fore feet have but three toes (Plate X, fig. 1); (3) the middle hoof of both fore and hind feet is noticeably larger than the hoof on each side of it; (4) the second upper premolar tooth is larger than that of *Epihippus* and it has the form of a true molar tooth (Plate XVIII, fig. 4). This animal, therefore, has six teeth in the grinding set and all are of similar size and shape. The first premolar remains small and unimportant.

In Plate I is reproduced a photograph of a group of these little three-toed horses exhibited at Field Museum. This group shows a small herd of the *Mesohippus* in its native surroundings. These animals have been modeled with great care and exactness by the well-known sculptor, Mr. Frederick Blaschke, whose masterly reproduction of the Neanderthal man has fixed so high a standard of excellence in reproducing extinct life by means of sculpture. This life-size group of little three-toed horses is placed in natural surroundings, such as they are believed to have inhabited when the "bad land" formation was gathering at the southern end of the Black Hills. The background of this group, painted by Field Museum's able staff

artist, Mr. Charles Corwin, represents the animals in surroundings of the Oligocene period, among sedgy shallows, bushes and trees such as are known to have lived at that time. The hills, towering in the background, are represented as a little more abrupt than they now appear, in order to make allowance for the leveling effect of erosion, which has been going on some thirty million years since *Mesohippus* roamed the Dakotas and Nebraska.

The four different kinds of horses which have so far been described have been found in four different geological formations which form a successive series. Each geological formation represents a period of time. From this we are led to conclude that these four different kinds of horses lived in four successive periods (Table, p. 15). The length of time from the beginning of the period of *Eohippus* to the end of the period of *Mesohippus*, according to the late Professor Barrell's estimate, is fifteen million years.[1]

SUMMARY

The four kinds of horses are similar in their anatomical structure. They are similar in the form of the head and of the molar teeth, in the number of vertebrae which bear ribs, in the form of the pelvis and of the shoulder blades, and in the proportions and construction of the legs. From these similarities it has been concluded that these animals are closely related, and so they are all included in one subdivision of the horse family. From their succession in point of time and their evident relationship, it has been further concluded that they are ancestral one to another. That is, it has been concluded that *Eohippus* is an ancestor of *Orohippus*, *Orohippus* an ancestor of *Epihippus*, and *Epihippus* in a broad sense an ancestor of *Mesohippus*.

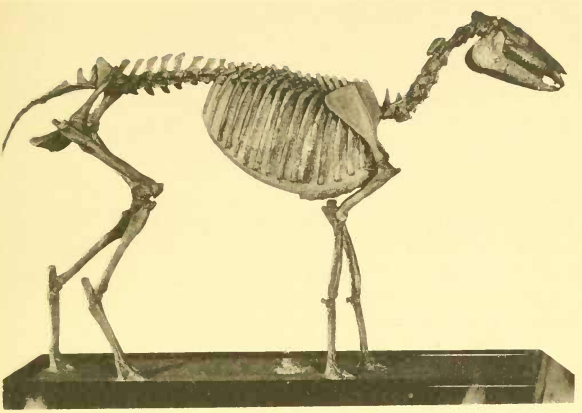
While the general characteristics of this line of animals are similar, as we have seen, there have appeared from time to time changes in various parts of the animal.

[1] Bull. Geol. Soc. Amer., 28, 1917, pp. 745–904.

Changes have probably taken place in all parts of the animal, but they are most noticeable in the teeth and in the feet. These parts are common points of variation in all of the horses. The change in the teeth is from those of smaller size and simpler pattern to those of larger size and of more complex pattern (Plate XVIII, figs. 1–4). This change gives to the animal a greater capacity for crushing his food. In like manner the changes in foot structure are from a broad, flat foot of four toes to a simpler foot of three toes (Figs. 3, 4). In this change the middle toe continually becomes stronger and more capable of bearing the weight of the animal; the side toes become weaker and less useful.

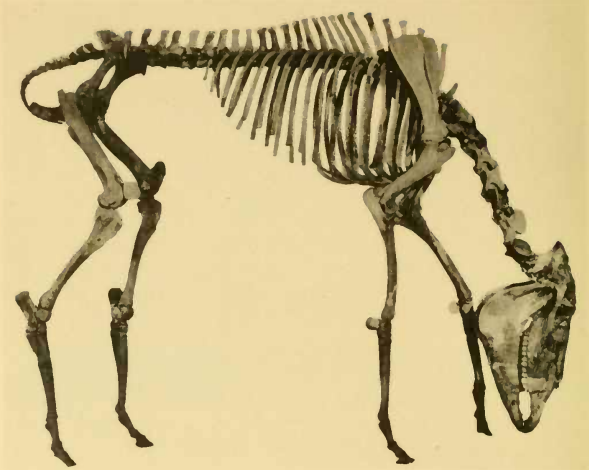
These four types of horses, succeeding one another as they do, in different geological periods, each a little larger than the one before and each changed a little from its nearest ancestor, give us the clue to the evolution of the horse. That is, progressive modification has taken place through minute changes which have extended over immense periods of time. These changes in the earlier members of the horse family indicate what may be expected in the later stages of horse history.

As a matter of fact, we shall now observe a rapid expansion in the horse's development. We shall see the horse of succeeding periods grow taller and larger of limb. We shall see him changed from a flat-footed, marsh-dwelling animal to a firm-footed, single-hoofed dweller of the plains. We shall see his face grow long, his eye become enclosed in a bony socket, his jaw-muscle thrust forward and his teeth change from the simple, short-crowned molars of a browsing animal to the long-crowned and complex grinding molars of a grass-feeder. With these changes in structure and habits we may now follow the horse's development as he passes from the simple and timid marsh-dweller to the strong, alert, and intelligent animal of modern times—the noblest and the most prized of all animals domesticated by the human race.

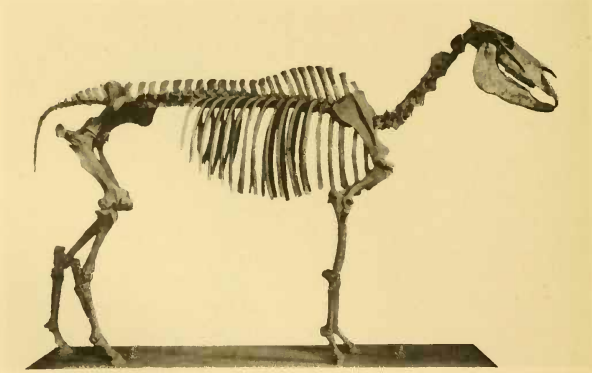


1. SKELETON OF THREE-TOED HORSE, *Mesohippus bairdii*
Photograph by American Museum of Natural History

2. RESTORATION OF THREE-TOED HORSE, *Mesohippus bairdii*
By Frederick Blaschke



1. SKELETON OF *Pliohippus leidyanus*, A ONE-TOED HORSE
Photograph by American Museum of Natural History



2. SKELETON OF *Equus scotti*, A TRUE HORSE. PLEISTOCENE OF TEXAS
Photograph by American Museum of Natural History

HISTORICAL ACCOUNT OF THE LATER FOSSIL HORSES

HORSES OF THE MIOCENE PERIOD

The rock systems which lie immediately above the Oligocene "bad lands" belong to the earliest or lower stages of the Miocene period. In the Pine Ridge of South Dakota and of western Nebraska this formation appears at the surface having a thickness of five hundred feet (Plate VI, fig. 1). Farther eastward in the same states the Middle Miocene formation appears. Along the streams of central Nebraska and southward in Kansas and in other more widely separated areas, the Upper Miocene formations appear at the surface. In these sandstone ledges and in loose sands are found the fossil remains of many members of the horse family.

Fossil horses of the Lower Miocene period may be divided into two series, indicated as the lowland horses and the upland horses. By some writers the lowland horses have been called the "forest horse." In the absence of known fossil forests it appears better to consider these animals as inhabitants of low, moist lands. The lowland horses of this time are known under the name of *Anchitherium*. Their structure was but little changed from that of the browsing animals of the Oligocene period. The crushing teeth had short crowns and a simple crown-pattern similar to that of the Oligocene horses. Animals of this kind reached a stature of thirty-six or more inches. The legs were long and stout and the neck correspondingly long so as to enable the animal to reach the ground. The middle toe bore most of the animal's weight, but the side toes were apparently used as an additional support when walking on soft or marshy lands.

The upland horse of the Lower Miocene period is known as *Parahippus*. This term may be interpreted as the "near horse." The animal was much more slender than the lowland horse of his time, not so tall, and probably more alert and active. The neck was moderately

long, the back had lost that rounded curve common to the Eocene horses, the shoulders were slightly elevated, and the outline of the back was similar to that of the modern zebras.

The head and jaws of *Parahippus* were rather slender, the muzzle narrow and the face noticeably longer than that of any of the earlier horses thus far described (Plate XVI, fig. 3). If we look closely at the skull we shall find that the eye socket in this animal is entirely enclosed by a bony ring, and that a narrow ridge extends forward from below the eye to give attachment for the muscle which closes the lower jaw. These are distinctly horse-like characteristics and justify the name of "near horse." Also, we find that the premolar teeth in this animal are slightly larger than the molars, that the crowns of all of the premolar and molar teeth have grown longer, and that a thin layer of white material known as the "cement" covers the enamel of the crown. The teeth have at this stage taken on the function of true "grinding teeth." In the cropping teeth the small depressions called the "cups," which are made use of by horsemen in judging the age of the animal, have appeared for the first time. The characteristics of tooth and of jaw which we have just observed are marks of the grass-feeding horses. Grass of the uplands is a much harder food than leaves or water plants, and a stronger mill is required to grind it. This need apparently has given rise to the larger attachment of the grinding muscles, the stronger premolar teeth with more ridges of enamel on the crown to do the grinding, and the greater length of tooth-crown to meet added wear at the grinding surface. The grinding movement of the jaws as well as the harder food has resulted in wearing away the chisel-like incisors so as to leave a broad crown surrounding the cup-like depression at the center. All of these changes are evidences of the modification of the mouth parts of the animal to meet the new stress laid upon them by a newly acquired feeding habit.

1. RESTORATION OF EXTINCT HORSE, *Equus abeli*, OF WESTERN EUROPE

2. DRAWING OF EXTINCT HORSE ON WALL OF CAVE DWELLING BY PRIMITIVE MAN OF EUROPE

Photograph by Henry Field

ONLY LIVING SPECIES OF WILD HORSE, *Equus przewalski*
Photograph by New York Zoological Society

In the Middle Miocene period the distinction between the lowland horses and the upland horses became much more marked. The lowland horses increased in size over those of Lower Miocene age until some of them grew to be as large as a small Indian pony. These horses are known under the name of *Hypohippus* or the "animal-akin-to-the-horse." By Professor H. F. Osborn they have been designated as the "forest horse."

While *Hypohippus* walked chiefly upon the larger middle hoof, the side toes were long and were of use in supporting the animal on soft ground. The structure of teeth and jaws remained almost as primitive as those of Oligocene horses. The eye socket was not enclosed on the backward side. The conservative nature of these animals is also evident in the small number of species found. At no time have there appeared more than two or three species of *Hypohippus*. Nevertheless, they continued to live in the lowlands which bordered the streams of the great plains. In the later division of the Miocene period they became widely distributed over the western states and reached eastern Asia.

Very different from the lowland horse was the desert horse, *Merychippus* (Plate XVII, fig. 1). This animal appears as a distinct type in the Middle Miocene period. The group included under this name is the most numerous and the richest in species of any genus of horses so far mentioned. No less than twenty-two species of these horses have been recorded. Their fossil remains are found among the wind-blown sands of the western plains. Their small size and stunted appearance suggest scant food and hard living. For that reason this animal has been designated as the "desert horse."

In *Merychippus* are found the beginnings of many horse-like characteristics. His stature is only a little greater than that of *Parahippus*. The head is proportionately large (Plate XVII, fig. 1), the legs are slender and the body and the neck are more horse-like. The

shoulders are more elevated so as to give to the back a slightly concave outline, or saddle. The neck is long enough to enable the animal to feed readily upon grass.

The tooth structure has so far advanced as to indicate that this was truly a grass-feeding animal (Plate XVIII, fig. 6). The crowns of the molars have grown long so as to provide against wear. As in modern horses the molar teeth were slowly pushed upward to meet the wear at the grinding surface. A heavy coating of cement overlies the enamel. The jaws have become deeper in order to make room for the long molar teeth. The face of the animal has become longer, the head behind the eyes relatively shorter. The head joins the neck at a right angle so that the nose projects more downward than forward. The two bones of the fore leg (ulna and radius) are separate in the young animal but in the adult animal they become joined together so as to form one bone.

The horses included under this genus are widely distributed. They have been found[1] in Florida, Texas, California, Montana and Oregon. The size varies from that of a wild ass to that of a small modern horse.

In the late Miocene period the one-toed horses appear for the first time. These animals are included under the name of *Pliohippus* (Plate XI, fig. 1). While they are usually spoken of as a one-toed animal, small and weak side toes are present in some species and absent in others. These horses are just on the border line where the side toes, long of little use to the animal, are being lost entirely. When the bones of the side toes are missing, the longer bones of the leg above the fetlock joint are called the "splints." These bones lie beside the metacarpal of the fore leg and beside the metatarsal of the hind leg and extend about three-fourths of the way to the fetlock joint. They are vestiges of the bones which were functional in the ancestral horses but which are being lost from disuse. These vestigial bones are still present in modern horses.

[1] W. D. Matthew, Quart. Rev. Biol., 1926.

Pliohippus is directly descended from one of the species of *Merychippus*.[1] The size of the animal is about the same as the larger species of that genus. The skull is large in proportion to the size of the body. Seventeen species are recognized by Osborn. They are found in Texas, California and other localities of North America.

HORSES OF THE PLIOCENE PERIOD

From the Pliocene formation of Texas there is known the very horse-like animal, *Plesippus*. This animal has been compared with the modern Arab horse in size and in general proportions. It is slightly shorter in the feet, and the body is smaller. The skull is remarkably horse-like. The teeth are similar to those of *Pliohippus* but have longer crowns. The fibula, or smaller bone of the middle section of the hind leg, is reduced to a vestige in this animal. The tibia now bears the entire weight. This is the last of the important changes in the skeleton which have marked the evolution of the horse.

The Pliocene period witnessed a loss of rainfall and an increase of cold in the old home of the horse family. The elevation of the Sierra Nevada mountain range slowly cut off the moisture-laden winds from the Pacific and left the Great Basin region quite arid. The Great Plains lying east of the Rocky Mountains had suffered a general uplift during the Miocene and the Pliocene periods and with it came an increase of cold and barrenness. In the face of this more rigorous climate, the Pliocene horses came into a fuller development.

Horses in this period became more numerous than at any previous stage. *Pliohippus* continued over from the last period as the most progressive of the upland horses. Two or three other branches of the upland stock are known to have been fairly abundant. The lowland horses in limited numbers survived until the middle of this period in North America.

[1] Matthew, *op. cit.*, fig. 1.

Only a few localities in Nebraska, Kansas and Texas of the Great Plains region, and correspondingly few areas west of the Rocky Mountains have preserved the remains of American horses of the Pliocene period. In these widely scattered localities have been found the remains of five or more different genera of horses and many times that number of species. Horses at that time appear to have been more numerous in North America than at any previous period. They were likewise finding their way into the Old World by means of land connections through the Bering Sea, and into South America by way of the isthmus.

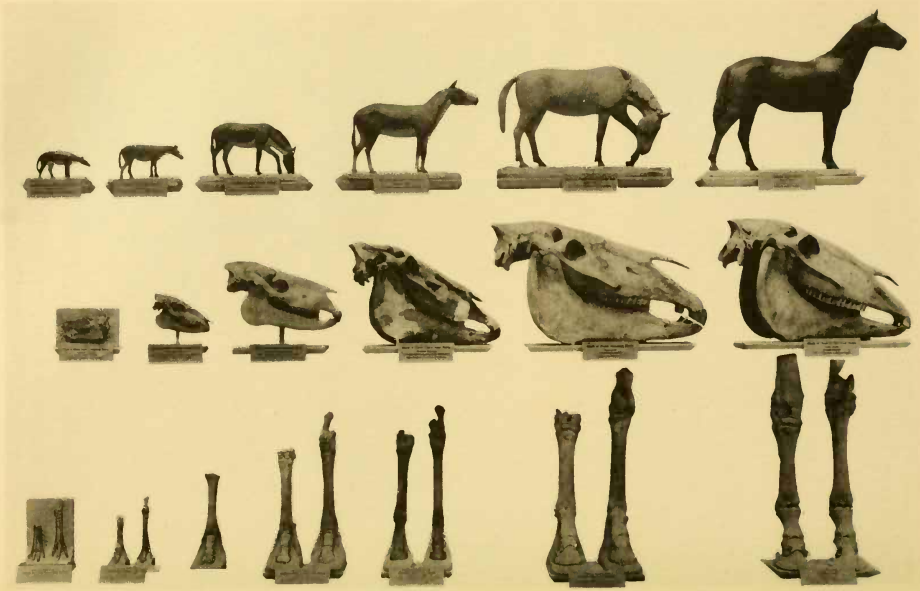
The lowland or forest horse was rapidly dying out. The main branches of the horse family were becoming thoroughly established in an open plains habit, some of them adapted to a desert life. The more advanced types were rapidly becoming one-toed animals, others of less progressive lines retained the cumbersome side toes. This was especially true of the tall and stilted lowland horse, *Hypohippus*, and of the smaller *Hipparion* line.

Certain side branches of the horse family which, like the lowland types, never reached the full development of the modern horse, are worthy of mention. Most notable among these is the sturdy and persistent line known as *Hipparion*. These animals are descended from the Miocene horse, *Merychippus*. They appeared in North America in the later stages of the Miocene period. They had relatively short-crowned, prismatic molars and three well-developed toes on fore and hind feet. Many of the species were small and slender of limb.

In early Pliocene time, species of *Hipparion* migrated to Asia, where they have long been known from fossil remains in the hills of central India. A little later these horses are known to have been abundant in southern and in western Europe. In mid-Pliocene time they were present in northern and central Africa. In all, thirty or more species have been recognized in various quarters of the world. Some of the European species were as small

MODERN WILD ANIMAL, *Equus kiang*, INTERMEDIATE BETWEEN HORSE AND ASS

2. LARGEST OF AFRICAN ZEBRAS, *Equus grevyi*
Photograph from specimen in Field Museum



THE EVOLUTION OF THE HORSE
An exhibit in Field Museum

and as slender as the pronghorn buck; others reached the size of the modern wild ass.

Another side branch of the horse family is known as *Protohippus*. This animal was restricted to North America and is known only from the Pliocene period. It is most nearly related to *Pliohippus*. All of the species are three-toed.

Horses of the Pleistocene Period

The Pleistocene was a period of alternating cold and warmth. It is often spoken of as the glacial period or the ice age. At times ice fields extended over the northern hemisphere well down into the temperate zone, where they remained for several thousand years. In turn, the interval of cold was succeeded by one of warmth in which the ice melted and vegetation and animal life flourished. These conditions caused plants and animals to migrate through stress of changed temperatures and oftentimes to be exterminated over large areas. In the regions scoured by the advancing ice-sheet much evidence of the extinct life was destroyed.

Members of the horse family which are entitled to be classed with the true horses appeared for the first time at the beginning of the Pleistocene period. Later in this period various species of true horses are known to have ranged over both North and South America, and over Asia, Europe and Africa. With the possible exception of the dog, they became the most widely distributed of all extinct mammals.

One of the earliest known species of the true horse, *Equus stenonis*, has been found in northern Italy. This was also one of the smallest of true horses and had the most primitive pattern of molar tooth. Certain species which were regarded by Matthew as almost equally primitive lived in North America during the earlier stages of the Pleistocene period. Along with them on this continent lived horses of other and more advanced species.

In the earlier part of this period horses are known to have lived in North America, Europe and Asia, in most regions not covered by the ice-cap. During the interval between the first and the second advance of ice, horses flourished in North America most abundantly. After the second advance of the ice so far as is now known they disappeared from this continent, but continued to flourish in the Old World. More than forty species of fossil horses of Pleistocene age are recorded from various regions throughout the world.

In the sands of Hays Springs, Nebraska, associated with the remains of camels and ground sloths are found the remains of a fossil horse, *Equus hatcheri*, as large as our common domestic horse. At Rock Springs, Texas, preserved in drifted sands, are found remains of the large-headed and stoutly built horse, *Equus scotti* (Plate XI, fig. 2). From the Port Kennedy bone caves of Pennsylvania are recorded the remains of two species of extinct horses, *E. complicatus* and *E. pectenatus*. In the valley deposits of Bolivia and in the pampa formations of Argentina are found remains of various species of extinct horses. They are known to have penetrated southward as far as the central provinces of Argentina. Records of horses from the great plains of northwestern North America are wanting, but the placer gravels near Dawson have yielded an interesting specimen which marks the supposed route of migration from North America to Asia.

The Pleistocene formations of Asia have so far been little explored. No fossil horses of this period have been reported from northern or eastern Asia. From the Siwalik Hills of northern India are known two species of true horses which are now determined as of Pleistocene age.[1] Later deposits of this period throughout Europe have yielded a number and variety of fossil horses which have

[1] W. D. Matthew, Critical Observations upon Siwalik Mammals, Bull. Amer. Mus. Nat. Hist., 1929, p. 441.

1

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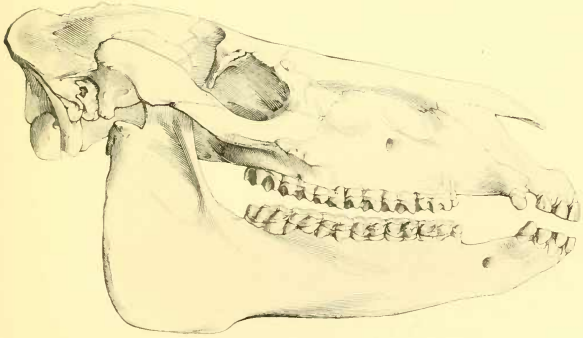


3

A COMPARATIVE STUDY IN SKULLS OF FOSSIL HORSES

One-third natural size

1

2

3

A COMPARATIVE STUDY IN SKULLS OF FOSSIL HORSES

One-sixth natural size

been classified[1] as follows: A small horse with short head, called the "desert horse of Europe"; a tall, slender horse with long head; and a large horse with heavy limbs and long head, called the "forest horse of Europe." Some twenty species in all have been recorded from that continent.

The true horse is held to have originated in North America and to have migrated to Asia and Europe by way of Bering Sea.[2] There, under conditions which admitted of a freer escape from the rigors of a glacial climate, these animals have survived until modern times. In North America, as has been observed, they disappeared entirely with the second advance of the ice-sheet.[3] Whether or not they may have lingered a little longer in South America is a matter of conjecture. Certain it is that native horses had disappeared entirely from the western hemisphere before the coming of white men. The stock from which horses were again introduced into North and South America was derived through domestication and intermingling of various wild species from Europe, Asia and Africa.

HORSES OF THE HUMAN PERIOD

The first evidence of horses in association with man is derived from western Europe. There, in caves of pre-Chellean age (the second interglacial epoch), the bones of horses and human artifacts are found intermingled. While this mingling of relics is not regarded as furnishing evidence of the conscious association of the horse with man, it at least signifies that horse and man lived in the same localities at the same period.

More convincing evidence that early man hunted and subsisted upon the flesh of horses is derived from an accumulation of bones and rubbish before a rock shelter

[1] F. B. Loomis, The Evolution of the Horse, 1926.
[2] Matthew, Quart. Rev. Biol., 1926.
[3] According to O. P. Hay, Carneg. Inst., 1923, p. 14.

of human habitation at Solutré, France.[1] It has been computed by Toussaint that the remains of as many as forty thousand horses are found at this place. With them are associated various stone implements of Aurignacian culture as well as the bones of many other animals. From the evidence of the human culture, the period of these horses is determined as the beginning of post-glacial time, twenty-five thousand years ago. The horses of Solutré were of a small, pony-like stock. Their bones are associated in various deposits of this time with a number of cold-climate animals, such as the reindeer, the musk-ox and the mammoth.

Of a somewhat later date (Magdalenian times) are drawings of horses on the walls of caves of western and southern France. Most of these drawings represent the short-bodied and stocky horse common to western Europe (Plate XII, figs. 1, 2). Antonius in his researches estimates that 90 per cent of all the cave drawings indicate this type of horse. The remaining 10 per cent are made up of figures of more slender "desert horses of Europe" and a larger and heavy-limbed "forest horse of Europe." There is in all of these drawings no evidence of gear or trappings such as would indicate that the horse had at that period been brought into domestication.

The earliest known domestication of the horse has been reported by Pumpelly from the old city of Anau, Russian Turkestan. Horse remains of a type similar to that still running wild in Mongolia are said to be abundant in these ruins.[2] By the stage of human culture existing at this time, this period of domestication is estimated by Duerst at 4500 B.C. From the recently excavated city of Kish, Mesopotamia, it has been reported that bones of an equine, either horse or ass, have been found beside the remains of chariots. The period of this domestication

[1] R. Lydekker, The Horse and Its Relatives, 1912.

[2] *Equus przewalski* or Przewalski's horse.

is placed at 3500 B.C.[1] In China the horse is generally known to have been in use at the beginning of recorded history, about 2000 B.C., first as a draught animal in chariots, and, at a later time, for riding. The horse is known to have appeared in Egypt at the time of the expulsion of the shepherd kings, about 1600 B.C. Monuments of the Mycenaean period in Greece represent horses and chariots in use in the fourteenth century. In 648 B.C. horses were first used in the Olympian games. Despite the fame of the modern Arab stock, horses were not introduced into Arabia until after our era. According to Professor Ridgeway, the ancestors of the modern Arab stock were derived from the Libyan plains of north Africa. The English thoroughbred is derived from a cross-breeding of the Barbary horse of Morocco and Algeria with the Arabian horse.[2]

The tarpan or Przewalski's horse of central Asia is the only wild species of true horse now living (Plate XIII). Of this animal Lydekker[3] writes: "Adult stallions of the Mongolian tarpan stand about 13.1 hands at the shoulders. As might be expected, its nearest domesticated representatives are the ponies of the same district. Their rough, untrimmed coats are very like those of their wild relatives, although they have developed long flowing manes, with forelocks, and tails which sweep the ground. These ponies are kept by the Buriats and other Mongolian tribes in millions and are very hardy and enduring."

A second species of wild equine is usually classed as intermediate between the true horses and the asses. This animal, the kiang (*Equus kiang*), inhabits the high plateaus of Tibet in Asia (Plate XIV, fig. 1). It is the largest of a group of related horses which have ranged over central Asia until comparatively recent

[1] H. Field, The Field Museum–Oxford University Expedition to Kish, Mesopotamia, 1923–1929, Field Mus. Nat. Hist., Leaf. Ser., 1929, p. 20.

[2] Lydekker, *op. cit.*

[3] *Op. cit.*, p. 107.

times. The animal is thirteen hands high, has a large head and relatively large ears, an erect mane, a reddish coat, grading light at the muzzle and on the belly. The hoofs are narrower than those of the domestic horse; chestnuts are present on the hind legs. Of this animal Loomis[1] writes: "These animals move freely at a fine springing trot over the rough rocks and broken ground of this high country, indicating that they possess hoofs of extreme hardness and lungs of tremendous power."

A smaller animal of lighter build and of more uniform coloring is the dziggetai (*Equus hemionus*) of Mongolia.

The wild ass mentioned in the Bible was known to the ancients as the onager. This is a somewhat paler-colored animal than the dziggetai. In modern times it inhabits the desert regions from Mongolia to Syria and Persia. It is smaller than any of the wild species above indicated, standing from eleven to eleven and one-half hands high.[2]

The African species of wild ass is distinct from that of Asia. It is usually designated as the true ass and by some writers is given a distinct name. The color is more uniform than that of the Asiatic variety of ass. This species is the source of the modern domesticated animal.

The zebras and quaggas are very similar to the wild asses in their structure and in their proportions. One species, *Equus grevyi*, is considerably larger than the ass and in some ways more horse-like, having a very large head, fringed ears and callosities on the fore legs (Plate XIV, fig. 2). The color bandings distinguish these animals in a striking way from all other living members of the horse family. By some zoologists they have been classified in a separate genus. Their skeletons are similar to those of the asses. The Grevy zebra of modern times ranges over the highlands of Abyssinia and of Somaliland. It is

[1] *Op. cit.*, p. 182.
[2] Lydekker, *op. cit.*

distinguished from the quagga by a different pattern of bandings. The quaggas range through south and east central Africa. Most of them have broad stripes on the head, neck and entire body, the legs being variable, some with bands and others without. In some of the southern forms, now nearly extinct, the hind quarters are dun colored and faintly or not at all banded.

EXTINCTION OF THE HORSE IN THE NEW WORLD

It is well established from the evidence which has been briefly outlined in the foregoing account of the horse family history that the horse flourished on the North American continent during four geological periods, now commonly estimated as covering forty-five million years. The horse then died out on this continent during the ice age while he possibly survived a little later in South America. It is also fully recorded in the history of the exploration and colonization of the American continents that a stock of closely related horses was again introduced from Europe into both North and South America. Horses of this stock have flourished in their new home as domestic animals and their descendants have, from time to time, run wild on both continents and in considerable numbers. The question as to why the native races of horses should have died out in regions which were later found to be well adapted to the habits and life of a similar introduced stock, has given rise to much speculation.

The extinction of the native American horses can hardly be attributed to the direct effect of the glacial cold, as the ice-sheet covered no more than half of North America and was limited to local areas in South America. Many contributing causes which may have been derived indirectly from increasing cold and moisture have been pointed out.[1] Among these are the effect upon the food supply, the increase of insect pests, and the effect upon fertility and reproduction.

[1] H. F. Osborn, Amer. Nat., 40, pp. 769–795.

Branches of the horse family had been dying out in North America before the ice age. The lowland horse and the numerous *Hipparion* line of upland horses had disappeared from both the Old and the New World during the preceding period. Other animals, such as the rhinoceros, had disappeared from the Great Plains region early in the Pliocene period. During the Pleistocene period the camels, a numerous family which had ranged over the same lands in North America and had fed upon the same kind of food as the horse, suffered extinction in North America as well as great reduction in South America. Only the smaller and less specialized members (the llamas and the vicuñas) have survived in South America until the present time. Other highly specialized animals, such as the saber-tooth tigers, the elephants and the mastodons, disappeared entirely from North America during the Pleistocene and the Recent periods. In short, the old and highly specialized lines of mammals in North America were dying out. The same gradual extinction was taking place among the native lines of South American mammals, and, to some extent, among those of Europe and Asia. In the latter continents a freer communication with tropical countries offered better opportunity for re-stocking from the south.

While horses of the genus *Equus* were widely distributed throughout North America in the Pleistocene period, there was among them an evident movement southward before advancing cold. Horses, in two successive waves of migration, are known to have reached the open pampas of South America. The first included the *Hippidion* and other related horses; the second, the *Equus* of various species. All of these horses died out in South America about the same time that the species of *Equus* disappeared from the plains of North America. By some writers it is held that the South American horse lingered a little longer.

It may be concluded that the horse, in Pliocene time, had reached a degree of racial old age which, as in the

camel of the same time, greatly lowered his adaptability to changed conditions of living. So, in the face of changing climate, changing food, and all of the unfavorable conditions which may have gone with them, the horse in America suffered extinction in the Pleistocene while his near relatives in Asia and his more distant relatives in Africa survived until modern times.

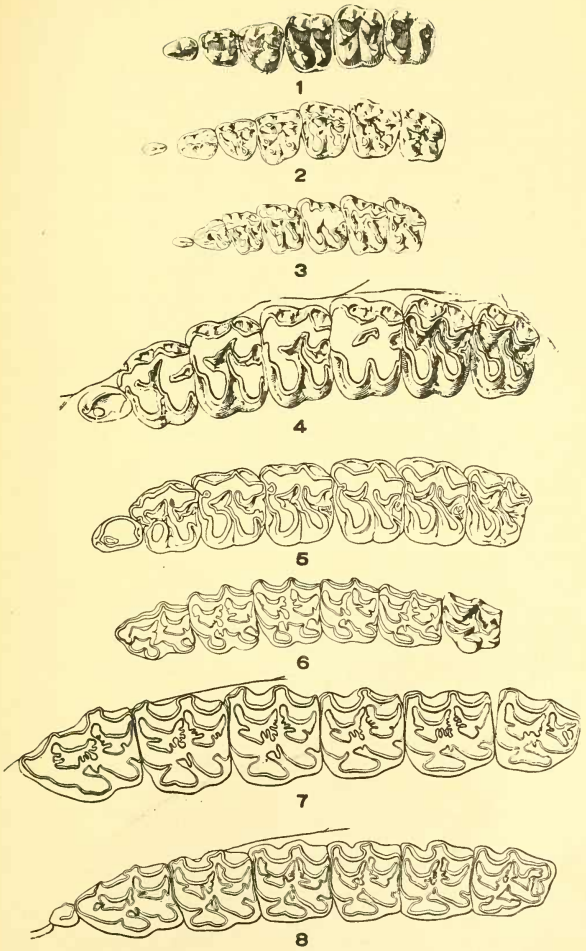
COMPARATIVE STUDIES IN THE EVOLUTION OF THE HORSE

Modifications in the structure of the horse skeleton will now be followed out in detail. Examples for comparison have been selected from the successive periods of horse history, using such animals as have been described in the historical account. By comparison of one specimen with another the more important changes which have taken place between the earliest and the latest members of the horse family may be followed out.

A photograph of an exhibit in Field Museum, illustrating the evolution of the horse, is reproduced in Plate XV. In this photograph are shown series of fossil skulls and feet of fossil horses in comparison with those of recent horses. They are arranged in the order of their historical sequence. While not all of the important steps in the evolution of the horse are represented by specimens in this series, most of them are so represented. A single genus, *Anchitherium*, which is not in the direct line of descent of the modern horse, is here made use of for comparison. A series of models made to scale, one-fifth actual size, illustrates the progressive changes in the animals as a whole.

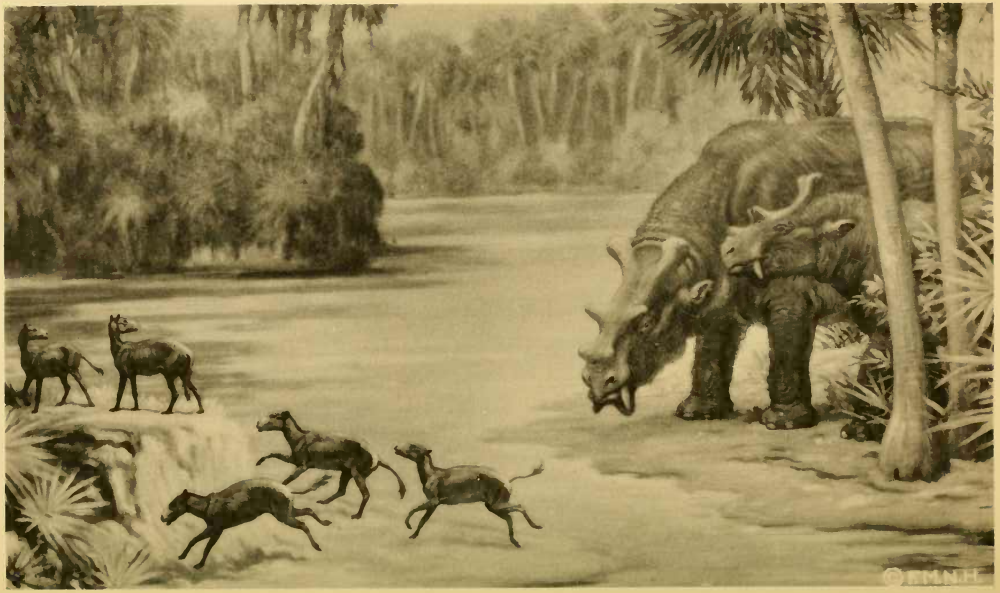
THE SKULL

The skull of *Eohippus venticolus* (Plate XVI, fig. 1) is five and one-half inches in length. In proportion it is long and narrow; the orbit is near the middle, dividing the skull into (1) a facial and (2) a cranial region, which are about equal in length. The center of the orbit is above the second molar tooth. The orbit is open backward; the arches are well developed, enclosing a wide temporal fossa. The sagittal crest is long and narrow, the profile of the skull straight. The bridle-gap is short and partly filled by the first premolar tooth.



SERIES OF TEETH OF FOSSIL HORSES

1–5 natural size, 6–8 one-half natural size



RESTORATION OF *Orohippus* AND *Uintatherium*

In *Mesohippus* (Plate XVI, fig. 2) the facial region of the skull has become longer than the cranial region. The arches and the sagittal crest are somewhat shorter; the orbit has become almost closed on the posterior side by the post-orbital process of the frontal bone. The bridle-gap is open; the lower jaw has become broader at the angle and tapers forward.

The face in *Parahippus* (Plate XVI, fig. 3) is one-fourth longer than the cranium; the center of the orbit is behind the third molar tooth. A prominent ridge (masseteric crest) has appeared below the eye and gives extended attachment to the masseter muscle. This is the first important change in mouth-structure which accompanied the change from a browsing animal to a grass-feeder.

The face in *Merychippus* (Plate XVII, fig. 1) is one-third longer than the cranium. The entire orbit lies behind the last molar tooth. The orbit at this stage is completely closed by a bony bar formed by the post-orbital process meeting the arch. The profile of the cranium is well rounded; the arch and the sagittal crest have become relatively short, the temporal fossa small. The teeth, as a second important change in mouth-structure due to changed feeding habit, have become long-crowned and covered with "cement."

The facial region in *Pliohippus* (Plate XVII, fig. 2) is so far elongated as to become almost double the length of the cranium. The orbit is firmly enclosed in a bony ring. The arch and the temporal fossa are correspondingly small; the occiput overhangs the condyles.

In the skull of the modern horse and in that of the extinct species of *Equus* (Plate XVII, fig. 3) the proportionate length of face and cranium is about the same as in *Pliohippus*. The cranium is more convex in outline; the masseteric crest extends as far forward as the last premolar. The important changes in the evolution of the skull are complete.

THE TEETH

In *Eohippus* (Plate XVIII, fig. 1) the upper molar teeth had short crowns and were implanted by four roots each. As seen from the crown view they were four-sided; each tooth had a grinding surface made up of two cone-shaped cusps on the outer margin and two oblique crests directed toward the inner margin. The upper premolars were all simpler in pattern and smaller than the molars; the third and fourth were sub-triangular in outline, having on the crown two cones and one oblique crest. They were implanted by three roots. The crown of the second premolar was elongate in the line of the dental series and bore two cones only. The first upper premolar was a simple conical tooth.

The tooth structure in *Orohippus* (Plate XVIII, fig. 2) is similar to that of *Eohippus*, except that the fourth upper premolar has changed to the form of a true molar.

In *Epihippus* (Plate XVIII, fig. 3) both the third and the fourth upper premolars have taken the form of true molars.

In *Mesohippus* (Plate XVIII, fig. 4) the second upper premolar tooth approaches the form of a true molar, though in this genus it has not quite reached the size of the succeeding tooth. The third molar is truly molariform. The first upper premolar is still a functional tooth; the gap between it and the second premolar has closed up.

In *Parahippus* (Plate XVIII, fig. 5) the three last upper premolars have grown to be larger and stronger teeth than the molars, and the inner crests are beginning to take the form of "crescents." The teeth in the adult animal show evidence of greater wear on the crown and cups first appear on the incisors as the result of wear.

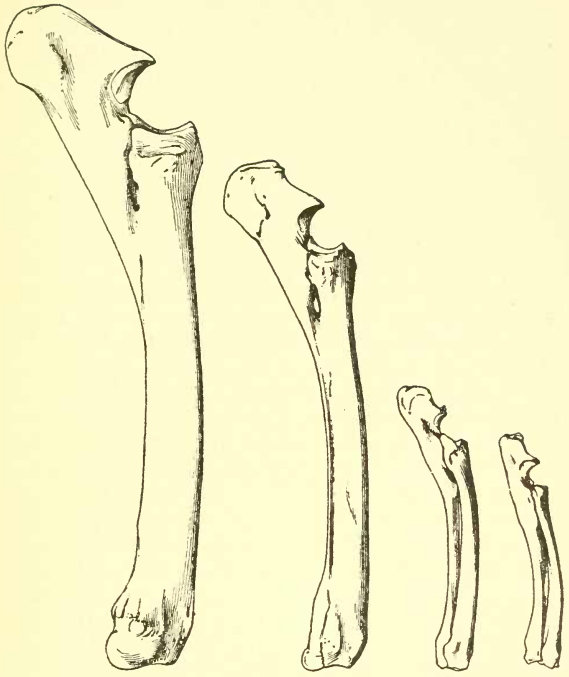
In *Merychippus* (Plate XVIII, fig. 6) the crowns of the teeth have grown long, and the enamel is covered with a whitish layer of "cement." Well-developed cups are found in the incisors. The first premolar is no longer

of use to the animal and in many specimens is entirely absent.

In the extinct species of *Equus* (Plate XVIII, figs. 7, 8) as well as in the modern horse the grinding teeth have long crowns fully covered with cement. Roots of these teeth appear after the animal is fully adult. Canine teeth are usually present in the male but absent in the female. The first premolar appears, rarely, as a vestige of the earlier functional tooth. The lower teeth pass through a similar evolutionary process in the same series of animals. Being less distinctive in structure, and consequently less reliable as a basis for comparative study, their progressive changes are not followed out here.

THE FORE LEG

In the four-toed horses *Eohippus* and *Orohippus* (Fig. 1, *a*) the ulna and the radius are separate bones of almost equal size. In the earlier three-toed horses *Mesohippus* and *Miohippus* (Fig. 1, *b*) the ulna has become much reduced in size but is still separate from the radius. In the later three-toed horses *Parahippus* and *Merychippus* (Fig. 1, *c*) the ulna has become attached to the radius throughout the greater part of its length and its shaft is reduced to a slight ridge on the surface of the radius. In the one-toed horses *Plesippus* and *Equus* (Fig. 1, *d*) the ulna is firmly joined to the radius at the upper and lower ends, and its shaft has disappeared entirely.

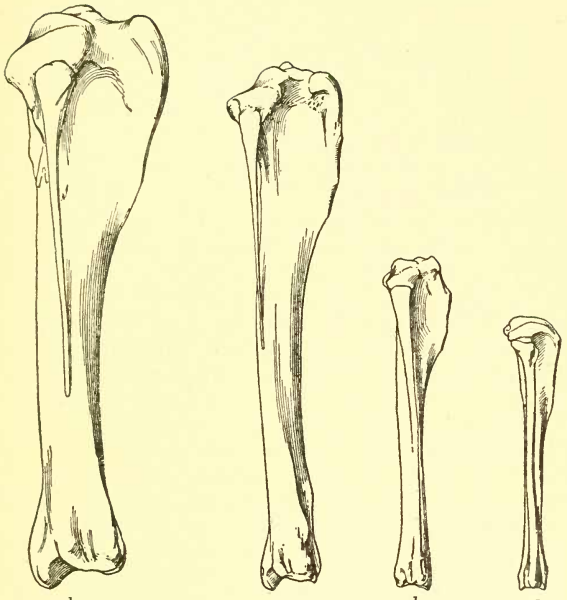


Courtesy of American Museum of Natural History

FIG. 1. Evolution of the Fore Leg, Principal Stages. (*a*) Four-toed horse, *Eohippus*, Eocene period. Leg bones separate and both strong. (*b*) Three-toed horse, *Mesohippus*, Oligocene period. Leg bones separate but closely attached. (*c*) Later three-toed horse, *Merychippus*, Miocene period. Leg bones nearly consolidated, shaft of ulna reduced to a thread. (*d*) One-toed horse, *Equus*, Pleistocene and Recent periods. Ulna completely consolidated with radius, shaft has disappeared.

THE HIND LEG

In the four-toed horses the fibula is a separate bone, articulating with the tibia at its extremities only (Fig. 2, *a*). In the earlier three-toed horses the fibula has become reduced in size and is joined to the tibia throughout its lower half (Fig. 2, *b*). In the later three-toed horses the fibula is reduced to a vestige only half of its original length, joined at the upper end and more or less free in the shaft (Fig. 2, *c*). The lower end of this bone becomes firmly joined to the tibia and continues to form part of the articulation at the joint. Essentially the same condition is found in the fibula of the one-toed horses (Fig. 2, *d*) except that the upper extremity is usually expanded into a rounded knob.



Courtesy of American Museum of Natural History

FIG. 2. Evolution of the Hind Leg, Principal Stages. (*a*) Four-toed horse, *Eohippus*, Eocene period. Tibia and fibula are separate. (*b*) Earlier three-toed horse, *Mesohippus*, Oligocene period. Fibula fused with tibia throughout lower half. (*c*) Later three-toed horse, *Merychippus*, Miocene period. Fibula incomplete and fused with tibia at both ends. (*d*) One-toed horse, Pleistocene and Recent periods. Lower end of fibula more firmly united with tibia.

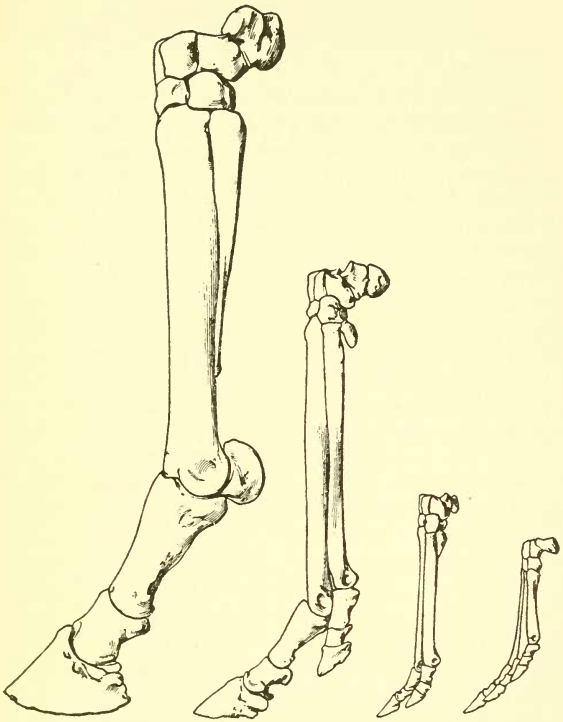
THE FORE FOOT

The progressive change in the fore foot of successive members of the horse family is the most important feature in their evolution. This change includes a reduction from a moderately short foot of four toes, all bearing functional hoofs which vary but little in size, to a foot composed of a single toe, borne upon an elongated metacarpal, and terminating in a single broad hoof. The change may be traced as follows:

In the fore foot of *Eohippus* (Fig. 3, *a*) digits II, III, IV, V are all present and in use. Digit I had disappeared from the fore foot of the horse at an earlier stage. Digit III is slightly longer and stronger than the others. Digits II and IV are about equal in size; digit V is the shortest and weakest of the series. The last joint of each digit, bearing the hoof, is longer than broad and tapers to a blunt point, slightly cleft. In the later four-toed horses *Orohippus* and *Epihippus* the third digit becomes progressively stronger, the fifth more reduced.

In *Mesohippus* (Fig. 3, *b*), the earliest three-toed horse, the middle toe has become stronger and apparently capable of bearing more of the animal's weight than the side toes. The fifth metacarpal is reduced to a vestige, though in one species a splint one-third the length of the adjacent fourth metacarpal remains.

In *Parahippus*, which is an intermediate three-toed horse, the third metacarpal and the joints of the third toe have become still stronger, the second and fourth metacarpals are further reduced in size and lie behind and against the middle one. The fifth metacarpal has been



Courtesy of American Museum of Natural History

FIG. 3. Evolution of the Fore Foot, Principal Stages. (*a*) Four-toed horse, *Eohippus*, Eocene period. Metacarpals short, weight borne upon pad under toes, "digitigrade." Middle toe only a little stronger than side toes. (*b*) Earlier three-toed horse, *Mesohippus*, Oligocene period. Metacarpals longer, weight borne upon hoofs, fourth toe reduced to splint. (*c*) Later three-toed horse, *Merychippus*, Miocene period. Middle toe grown stronger to bear weight, side toes reduced to "dew-claws." (*d*) One-toed horse, *Equus*, Pleistocene and Recent periods. Middle carpal or "cannon bone," grown larger in every successive stage, may now be regarded as third section of leg. Lateral toes reduced to splints.

reduced to a mere vestige at the wrist joint. The bone supporting the hoof has grown broader and has developed the side wings which are prominent in later horses.

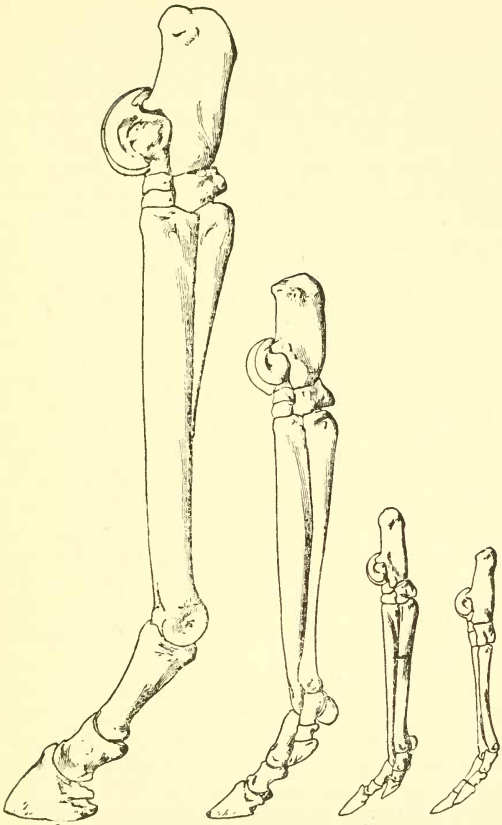
In *Merychippus* (Fig. 3, *c*), one of the later three-toed horses, the third metacarpal has become still stronger and rounded in the shaft. The second and fourth metacarpals are correspondingly slender, and a vestige of the fifth still remains. The middle toe has grown stronger so as to bear the weight of the animal; the side toes are so short as to be of service only when the animal is walking upon soft ground.

In the later species of *Pliohippus* and likewise in *Plesippus*, the side toes have disappeared entirely, the weight is borne by the middle toe alone, and the hoof bone has become as strong as that in modern asses and zebras. The side metacarpals have become reduced to splints which extend three-fourths of the length of the middle metacarpal.

In the extinct species of *Equus* (Fig. 3, *d*), and in the modern domestic horse, the splint bones are further shortened, barely reaching the middle of the third metacarpal, which in modern horses is known as the "cannon bone."

THE HIND FOOT

A similar reduction from three functional toes and two splints, to two splints and one functional toe has taken place in the hind foot of the same series of animals (Fig. 4, *a–d*). This change takes place by slow degrees and over the same periods of time as the corresponding changes in the fore feet.



Courtesy of American Museum of Natural History

FIG. 4. Evolution of the Hind Foot, Principal Stages. (*a*) Four-toed horse, *Eohippus*, Eocene period. Metacarpals short, all bear functional toes. (*b*) Three-toed horse, *Mesohippus*, Oligocene period. Middle toe enlarged, side toes reduced. (*c*) Later three-toed horse, *Merychippus*, Miocene period. Middle toe stronger, hoof larger, side toes shorter, side metatarsal slender. (*d*) One-toed horse, *Equus*, Pleistocene and Recent periods. Middle metatarsal strong and rounded, middle hoof broad and bearing all of weight, side metatarsals reduced to splints.

CONCLUSIONS

The conclusions to be drawn from the foregoing pages are these: The records contained in fossil remains supply us with unquestionable evidence of animals which lived in past ages. A study of such evidence shows that members of the horse family have lived through five successive geological periods. By a competent authority whose conclusions are generally accepted, these five periods are estimated at forty-five million years. During that time members of the horse family grew up from an ancestor no larger than a fox to the size of the horse as we now know him, and became distributed over almost the entire world.

The genealogy of the horse does not follow a simple line of descent but branches out in many directions. Various branches of the family flourished for long periods in different parts of the world and died out without giving rise to true horses. Even among the few living species of the family there appears such variety as is seen in the domestic horses, wild ponies, zebras, quaggas, and asses. A small but a continued variation appears to have been the rule.

Comparison of the fossil remains of horses which have lived in different periods shows that certain changes in the animal structure have taken place. Comparison of a series of such remains from a number of successive periods shows that these changes were tending in certain definite directions. These changes had to do with some of the most essential parts of the animal's mechanism.

The more important changes which are evident in all lines of horse descent are: (1) an increase in size of the animal; (2) a change in the proportions of the head with special reference to the jaws and the teeth; (3) a change from a broad-footed animal which walked upon a pad beneath the toes to one which walked upon the ends of

his toes, and finally upon the end of a single toe with a broad hoof; (4) a change from an animal with shorter leg of two sections to one of longer leg with foot extended so as to form a third section of the leg, and with the muscles gathered near the body so as to give greater capacity for running; and, finally, (5) the change in habit from a low-land or woodland animal to the strong and swift-footed inhabitant of the open plains. These changes are the important features of the evolution of the horse.

The records of horse evolution have been so well kept by nature in the rocks, the clays and the sands; the evidence adduced from them is so unmistakable; and the conclusions drawn from this evidence are so well vouched for by scientific workers of every land, that there can be no question of the accuracy of the recorded history of the horse. If this evidence has been well presented here and is properly understood, it should be convincing.

The evolution of the horse is but one example of the workings of natural processes of evolution. Many similar examples might be drawn from the extinct animals of North America alone. The camels, the titanotheres, the rhinoceroses, the mastodons, and many others whose names are less familiar, have had a similar history. One after another they have come up from small and obscure ancestry, have attained large size and a high degree of specialization, have roamed this continent in large numbers, and have died out like the American horse. Our museums are stored with their fossil remains. Every one of them has a story to tell—a story only a little less connected because as yet less perfectly known; but when it is fully known it will be as telling and as convincing as that of the evolution of the horse.

ELMER S. RIGGS

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PRINTED IN THE UNITED STATES OF AMERICA
BY FIELD MUSEUM PRESS