APPENDIX.

ART. XXVIII.—*Notice of New Equine Mammals from the Tertiary Formation;* by O. C. MARSH.

THE explorations of the Yale College party in the Tertiary deposits of the West, during the past season, brought to light many equine remains; some of which prove to be new, and others throw considerable light on the forms already made known by previous investigations. In the present communication some of the more important results obtained are briefly presented, those relating to the genealogy of the modern horse being of special interest.

Orohippus Marsh.

This Journal, iv, p. 207; v, p. 407.

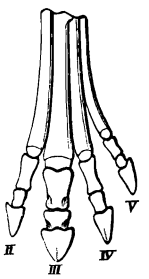
The equine mammals of the American Eocene are at present represented by three species of the genus *Orohippus*, the main characters of which have already been pointed out by the writer. Additional material clears up several doubtful points in its structure. This genus is nearly related to *Anchitherium*, but differs especially in having four functional digits in the manus, and in the absence of an antorbital fossa. The orbit is not enclosed behind. The dentition is very similar to that of *Anchitherium*, but the first upper premolar is proportionally larger, and the succeeding premolars are smaller. The median posterior tubercle of the molars is wanting. The first lower premolar was small, and the rest of the lower molar series closely resemble those in *Anchitherium*. There is long distema. The canine is large, and near the incisors. The crowns of the grinders are very short, and without cement. The dental formula is as follows:

$$\text{Incisors } \frac{3}{3},\ \text{canines } \frac{1}{1},\ \text{premolars } \frac{4}{4},\ \text{molars } \frac{3}{3}.$$

The skeleton of *Orohippus*, in its general features, is decidedly equine, and this is particularly manifest in the limbs. The scapula has a prominent acromial process, which is compressed and decurved, as in some of the carnivores. The humerus is short and stout. Its head is large, and the bicipital groove

narrow and deep. The great tuberosity is elevated, and compressed. The distal end of the humerus is small. The radius and ulna are distinct. The latter is larger than in *Anchitherium*, and entire throughout its whole length. The carpal bones are eight in number, and somewhat similar to those of the Tapir, although the trapezium is proportionally much smaller.

All the digits of the manus, except the first, are well developed, as shown in the accompanying figure of the left fore-foot of *Orohippus agilis* Marsh. The third digit is the largest, and its close resemblance to that of the horse is clearly marked. The terminal phalanx, or coffin bone, has a shallow median groove in front, as in many species of this group in the later Tertiary. The fourth digit exceeds the second in size, and the fifth is much the shortest of all. Its metacarpal bone is considerably curved outward. In the pes of this genus, there are but three digits. The fourth metatarsal is much larger than the second. The astragalus has its neck more elongated than in *Anchitherium*, and the face for the cuboid is small. The tibia and fibula are distinct. The cervical vertebræ of *Orohippus* are rather short, and moderately opisthocœlous.



Orohippus major, sp. nov.

The largest species of this genus is indicated by part of an upper jaw with three molars, and the greater portion of a lower jaw with teeth pertaining to another individual. In the former specimen, the intermediate lobes of the molars are less developed than in the species already described, while the antero-posterior buttress is more elevated. The lower jaw is stout, and there is a strong basal ridge on the outer face of the lower molars.

Measurements.

Space occupied by three upper true molars,	24·[mm]·
Antero-posterior diameter of last upper molar,	8·5
Transverse diameter,	10·
Antero-posterior diameter of penultimate upper molar,	8·5
Transverse diameter,	11·
Extent of four posterior teeth of lower jaw,	33·5
Antero-posterior diameter of last lower molar,	10·5
Transverse diameter,	5·
Antero-posterior diameter of last lower premolar,	7·5
Depth of jaw below middle of this tooth,	14·

This species was about as large as a fox. The remains of it at present known are from the Eocene of Wyoming.

The animals of this genus constitute a distinct family that may be called *Orohippidæ*. The other known species are as follows:

Orohippus gracilis Marsh.

(*Anchitherium gracile* Marsh;) this Journal, ii, p. 38, 1871.

Orohippus pumilus Marsh.

This Journal, iv, p. 207, 1872. (? *Helotherium procyoninum* Cope, Proc. Am. Phil. Soc., xii, p. 466, Feb., 1873.)

Orohippus agilis Marsh.

This Journal, v, p. 407, 1873.

All the animals of this genus now known were quite diminutive, the largest hardly exceeding a fox in size. They are all from the Eocene of Wyoming and Utah.

Miohippus annectens, gen. et sp. nov.

The present genus represents an intermediate form between *Orohippus* and *Anchitherium*. It differs from the former in having but three digits in the manus, and from the latter in the absence of an antorbital fossa, and in the more complete separation of the intermediate lobes of the upper molars. Its dental formula is apparently the same as *Orohippus*. The incisor teeth are small, and the canines large, those below being close to the incisors. The first upper premolar is of moderate size, and the second larger than the last true molar. In the upper molars, the basal ridge rises into a tubercle near the middle of the anterior border. The premaxillaries are slender. The radius and ulna are free, or only loosely united, but the fibula is fused to the tibia at its distal end. The second and third cuneiform bones are distinct. There are three digits in the manus, and three in the pes, all of which reached the ground. They appear to have been more nearly of equal size than in *Anchitherium*.

In the present species the orbit is large, and its anterior margin is directly above the front of the last upper molar. The first upper premolar had two fangs. The enamel of all the teeth preserved is quite smooth. The upper premolars and most of the molars have a prominent compressed tubercle between the inner cusps, but no inner basal ridge. This species differs widely from any hitherto described, with the possible exception of *Anchitherium Condoni* Leidy.* The latter species was founded on an imperfect upper molar tooth, which probably belongs to the genus *Miohippus*. The enamel of this molar is quite rugose, the small cusp behind the posterior crest is parallel with the posterior basal ridge, and the inner tubercle between the transverse crests is entirely wanting. This tooth

* Proc. Acad. Nat. Sci. Philadelphia, 1870, p. 112.

is also proportionally broader than the corresponding teeth of the present species, and hence the two must be regarded as distinct.

Measurements.

Space occupied by four upper premolars,	61·	mm.
Extent of three upper true molars,	46·	
Antero-posterior diameter of first upper premolar,	13·5	
Antero-posterior diameter of second upper premolar,	19·	
Transverse diameter,	18·	
Antero-posterior diameter of last upper molar,	14·	
Transverse diameter,	19·5	
Length of calcaneum,	68·	
Length of astragalus,	32·	
Antero-posterior diameter of tibia at distal end,	26·	
Transverse diameter,	33·	

All the known remains of this species are from the Miocene of Oregon. They indicate an animal somewhat exceeding a sheep in size, and with longer limbs.

Anchitherium anceps, sp. nov.

The Miocene deposits of Oregon contain another species of solipeds, smaller than the one just described, and apparently belonging to the genus *Anchitherium*. The skull has a large antorbital fossa, and the molar teeth agree essentially with those of that genus. The limbs, so far as known, were also similar. The first upper premolar has two fangs, and is well développed. The infra-orbital foramen is above the center of the third premolar. The present species most nearly resembles *Anchitherium Bairdi* Leidy, from the Miocene east of the Rocky Mountains. It differs, however, aside from the larger size, in the following particulars: the skull is depressed between the orbits; the molar teeth extend farther back below the orbit; the external cusps of the upper molars have their buttresses much stouter, and the concavities between them divided by more prominent vertical ridges.

Measurements.

Space occupied by four upper premolars,	47·5	mm.
Antero-posterior diameter of first upper premolar,	9·	
Antero-posterior diameter of second upper premolar,	13·	
Transverse diameter,	13·	
Antero-posterior of last upper premolar,	13·	
Transverse diameter,	15·5	
Antero-posterior diameter of last lower molar,	17·	
Transverse diameter,	8·	
Extent of upper molar series (second specimen),	82·	
Extent of three upper true molars,	37·	

The remains of this species indicate an animal about as large as a sheep. The specimens on which the above description is

mainly based, were presented to Yale College Museum by the Rev. Thomas Condon, of Oregon.

Anchitherium celer, sp. nov.

The smallest species of *Anchitherium* from the American Tertiary is indicated by some fragmentary remains in the Yale Museum, from the Miocene of Nebraska. These fossils pertain to a fully adult animal, which was about two-thirds the size of *Anchitherium Bairdi*. The orbit is placed well forward. The ridge below it is especially prominent, and much elevated above the molar teeth. The crowns of the latter are remarkably short. The four posterior molars have their inner margins on a line. The last upper molar is quite small.

Measurements.

Space occupied by last four upper molars,	37· mm.
Extent of three upper true molars,	27·
Antero-posterior diameter of last upper premolar,	10·
Transverse diameter,	13·
Antero-posterior diameter of last upper molar,	8·5
Transverse diameter,	12·
Distance of lower margin of orbit above last upper molar,	20·

The type specimen of the species was presented to Yale College Museum by Capt. W. A. Jones, of the U. S. Engineers.

Protohippus parvulus Marsh.

(*Equus parvulus* Marsh, this Journal, xlvi. p. 374, 1868.)

A reëxamination of the remains of this species originally described, and of the other fossils found with them, clearly indicates, as at first suspected, that this diminutive animal was not a true *Equus*, and there can now be but little doubt that it belongs in the genus *Protohippus* of Leidy, as at present understood. With the limb bones preserved, an upper molar tooth was found, which doubtless pertained to the same animal, although it is rather larger in proportion than the teeth of some allied species. The crown of this tooth is very short, and the arrangement of the enamel particularly simple. The inner lakes have no folds, and agree in form with those of *Protohippus* (*Merychippus*) *insignis* Leidy. The anterior lake, at its inner posterior angle, is connected by a narrow outlet with the main transverse valley. The inner anterior column is a broad oval in outline, and is connected with the antero-median column. This molar is from near the middle of the series, and measures 15^{mm}· antero-posterior diameter. Other fragmentary teeth indicate that the incisors were very small, and the canines large.

The bones of the feet preserved, which may with considerable certainty be referred to the same individual, imply that the manus and pes had the lateral digits developed, as in *Hipparion*.

The known remains of this species indicate an animal about two and a half feet in height. The specimens described are from the Pliocene beds at Antelope Station, Nebraska. Other remains of the same species were found by the writer, last year, on the Niobrara River, in the same geological horizon.

Pliohippus pernix, gen. et sp. nov.

A new genus of solipeds, allied to *Equus*, is well represented in the Yale Museum by two partial skeletons, with the more important portions preserved, and by numerous fragmentary remains. This genus closely resembles *Protohippus* Leidy in its dentition, but differs in the absence of lateral digits, which are only represented by slender splint bones. From the true *Equus*, the present genus may be distinguished by the presence of a large antorbital fossa; by the functional first upper premolar; and by a different composition of the crowns of the upper molars. The dental formula of *Pliohippus* is as follows:

$$\text{Incisors } \frac{3}{3}, \text{ canines } \frac{1}{1}, \text{ premolars } \frac{4}{3}, \text{ molars } \frac{3}{3}.$$

The incisors have the characteristic pit of the modern horse. The molars have short crowns, with distinct fangs. The skull is comparatively short, and the orbit is closed behind. The ulna is not entire, and its extremities are ankylosed to the radius. The distal end of the fibula has coalesced with the tibia. On the radial side of the carpus, there is a small ossicle which appears to represent the trapezium. On the opposite side, attached to the unciform, there was a rudiment of the fifth metacarpal.

The present species was about the size of the ass. The skull is larger, and has a deep irregular fossa in front of the orbit. The molar teeth have very short crowns, and long fangs. The folds of the enamel are very simple, and there are none in the inner lobes. The limbs were slender, and more elongated than in the ass. The ungual phalanges are broader, and slightly cleft at their extremities. The femur has the fossa above its outer condyle unusually deep. The cuboid facet on the astragalus is larger than in most equines.

Measurements.

Extent of four upper premolars,	88· mm.
Antero-posterior diameter of first upper premolar,	13·
Antero-posterior diameter of second premolar,	31·
Extent of three upper true molars,	68·
Antero-posterior diameter of last upper molar,	28·
Extent of lower molar series,	146·
Extent of last three lower molars,	72.
Length of radius,	253·

Width of proximal end,	49·	mm.
Width of articulation of distal end,	40·	
Length of third metacarpal,	189·	
Length of first phalanx of third metacarpal,	55·	
Length of second phalanx,	25·	
Length of third phalanx,	38·	
Width of third phalanx,	50·	
Length of calcaneum,	77·	
Length of astragalus,	41·	
Length of third metatarsal,	208·	

The specimen here described was exhumed by the writer, in June last, from the Pliocene sands of the Niobrara River, Nebraska.

Pliohippus robustus, sp. nov.

A second species of the genus *Pliohippus* is indicated by part of a skeleton with portions of the skull and teeth of one individual, and apparently by fragments of others. This species was nearly the same size as that last described, but the limbs were shorter and stouter. The first upper premolar is much larger, and the upper molars are longer, and much curved. The crowns of these teeth have a very similar arrangement of the enamel, but the folds are more complex.

Measurements.

Extent of four upper premolars,	98·	mm.
Antero-posterior diameter of first upper premolar,	18·	
Antero-posterior diameter of second premolar,	29·	
Extent of three upper true molars,	73·	
Transverse diameter of humerus at distal end,	54·	
Transverse diameter of radius at proximal end,	50·	
Transverse diameter of distal end,	50·	
Length of third metacarpal,	178·	
Width of proximal end,	33·	
Width of distal articular face,	29·	
Length of first phalanx of third metacarpal,	54·	
Length of second phalanx,	30·	
Length of third phalanx,	36·	

The known remains of this species were found by the writer, last summer, in the Pliocene strata of the Niobrara River.

Protohippus avus, sp. nov.

A number of teeth from the Pliocene beds of Oregon indicate a well marked species, which may provisionally be placed in the genus *Protohippus*, although they differ so widely from those already described that additional remains will probably prove them to be generically distinct. The most of these specimens are apparently all from one individual, and consist of a nearly complete series of upper and lower molars, and one

incisor. The molar teeth have very short crowns, and are inserted by distinct fangs. The enamel is covered with a thick coat of cement. The molars are considerably worn, and the pattern of the enamel thus produced nearly resembles that in the corresponding teeth of *Anchitherium*, with which the present teeth agree, also, in form and arrangement. The main peculiarity of the upper molars is, that in all of them the anterior lake opens into the transverse valley, while the outer lake is distinct, and much contracted. The outer concavities of the external lobes are without any median elevation. The posterior inner cone is larger than the one in front. All the lower molars have an outer basal ridge. The middle teeth are the largest of the series. The second premolar resembles in form the same tooth in *Anchitherium*, but the anterior buttress is less distinct. There are six lower molars, the last premolar being the largest of the series. The first premolar had its anterior lobe unworn, and much elevated above the level of the grinding surface. The fore and aft diameter of the lower molars is unusually short. The enamel of these teeth is strongly rugose, more so than that of the upper molars.

Measurements.

Space occupied by six upper molars,	110·mm.
Space occupied by three upper premolars,	57·
Antero-posterior diameter of second upper premolar,	23·
Transverse diameter,	22·
Antero-posterior diameter of last upper molar,	17·
Transverse diameter,	22·
Extent of three lower premolars,	57·
Antero-posterior diameter of first lower premolar,	20 5
Transverse diameter,	15·
Antero-posterior diameter of first lower true molar,	18·
Transverse diameter,	16·

For the type specimen of the species, I am indebted to Rev. Thomas Condon, of Oregon, who first explored the Pliocene strata of that State.

Anchippus brevidens, sp. nov.

The genus *Anchippus* Leidy was founded on a single upper molar tooth from strata, in Texas, supposed to be Miocene.* Several teeth obtained by the Yale party in the Pliocene of Oregon clearly belong to the same genus, but indicate a distinct species. These teeth agree in the general structure of their crowns with the type of *Anchippus Texanus*, but the antero-median lobe is placed further forward, and hence its worn surface is not in the same line with that of the antero-internal lobe. The posterior crescentoid tubercle, also, is isolated, and

* Proc. Acad. Nat. Sciences, Philadelphia, 1868, p. 231.

wears into an ear-shaped lobe, enclosing a pit filled with cement. The crowns of these molars are unusually short, even when unworn. They all have distinct fangs, and their enamel is covered with cement. The outer lobes have only a faint indication of a median ridge on their concave faces. The buttresses that enclose these faces are prominent.

Measurements.

Antero-posterior diameter of first upper true molar, ...17·5mm.
Transverse diameter, ... 22·
Antero-posterior diameter of last upper molar, ...17·
Transverse diameter, ... 21·5
Height of unworn crown of last upper molar, ...15·

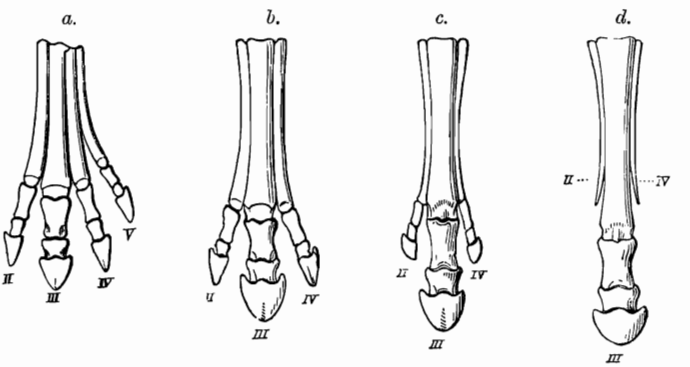
The specimens here described indicate that the genera *Anchippus* and *Hypohippus*, established by Dr. Leidy, are nearly related, and will probably prove to be identical.

The large number of equine mammals now known from the Tertiary deposits of this country, and their regular distribution through the subdivisions of this formation, afford a good opportunity to ascertain the probable lineal descent of the modern horse. The American representative of the latter is the extinct *Equus fraternus* Leidy, a species almost, if not entirely, identical with the old world *Equus caballus* Linn., to which our recent horse belongs. Huxley has traced successfully the later genealogy of the horse through European extinct forms,* but the line in America was probably a more direct one, and the record is more complete. Taking, then, as the extremes of a series, *Orohippus agilis* Marsh, from the Eocene, and *Equus fraternus* Leidy, from the Quaternary, intermediate forms may be intercalated with considerable certainty from the thirty or more well marked species that lived in the intervening periods. The natural line of descent would seem to be through the following genera:— *Orohippus*, of the Eocene; *Miohippus* and *Anchitherium*, of the Miocene; *Anchippus*, *Hipparion*, *Protohippus*, and *Pliohippus*, of the Pliocene; and *Equus*, Quaternary and recent.

The most marked changes undergone by the successive equine genera are as follows: 1st, increase in size; 2nd, increase in speed, through concentration of limb bones; 3d, elongation of head and neck, and modifications of skull. The increase in size is remarkable. The Eocene *Orohippus* was about the size of a fox. *Miohippus* and *Anchitherium*, from the Miocene, were about as large as a sheep. *Hipparion* and *Pliohippus*, of the Pliocene, equalled the ass in height: while the size of the Quaternary *Equus* was fully up to that of the modern horse.

* Anniversary Address, Geological Society of London, 1870.

The increase of speed was equally marked, and was a direct result of the gradual modification of the limbs. The latter were slowly concentrated, by the reduction of their lateral elements and enlargement of the axial one, until the force exerted by each limb came to act directly through its axis, in the line of motion. This concentration is well seen, e. g., in the fore limb. There was, 1st, a change in the scapula and humerus, especially in the latter, which facilitated motion in one line only; 2nd, an expansion of the radius, and reduction of the ulna, until the former alone remained entire, and effective; 3rd, a shortening of all the carpal bones, and enlargement of the median ones, ensuring a firmer wrist; 4th, an increase in size of the third digit, at the expense of those on each side, until the former alone supported the limb. The latter change is clearly shown in the following diagram, which represents the fore feet of four typical genera in the equine series, taken in succession from each of the geological periods in which this group of mammals is known to have lived:



a. Orohippus (Eocene); *b. Miohippus* (Miocene); *c. Hipparion* (Pliocene); *d. Equus* (Quaternary).

The ancient *Orohippus* had all four digits of the manus well developed. In *Miohippus*, of the next period, the fifth toe has disappeared, or is only represented by a rudiment, and the limb is supported by the second, third, and fourth, the middle one being the largest. *Hipparion*, of the later Tertiary, still has three digits, but the third is much stouter, and the outer ones have ceased to be of use, as they do not touch the ground. In *Equus*, the last of the series, the lateral hoofs are gone, and the digits themselves are represented only by the rudimentary splint bones.* The middle, or third, digit supports the limb, and its size has increased accordingly. The corresponding

* The modern horse occasionally has one of the ancestral hoofiets developed, usually on the fore foot.

changes in the posterior limb of these genera are very similar, but not so manifest, as the oldest type (*Orohippus*) had but three toes behind. An earlier ancestor of the group, perhaps in the lowest Eocene, probably had four toes on this foot, and five in front. Such a predecessor is as clearly indicated by the feet of *Orohippus*, as the latter is by its Miocene relative. A still older ancestor, possibly in the Cretaceous, doubtless had five toes in each foot, the typical number in mammals. This reduction in the number of toes may, perhaps, have been due to elevation of the region inhabited, which gradually led the animals to live on higher ground, instead of the soft lowlands where a polydactyl foot would be an advantage.

The gradual elongation of the head and neck, which took place in the successive genera of this group during the Tertiary period, was a less fundamental change than that which resulted in the reduction of the limbs. The process may be said to have already began in *Orohippus*, if we compare that form with other most nearly allied mammals. The diastema, or "place for the bit," was well developed in both jaws even then, but increased materially in succeeding genera. The number of the teeth remained the same until the Pliocene, when the front lower premolar was lost, and subsequently the corresponding upper tooth ceased to be functionally developed. The next upper premolar, which in *Orohippus* was the smallest of the six posterior teeth, rapidly increased in size, and soon became, as in the horse, the largest of the series. The grinding teeth at first had very short crowns, without cement, and were inserted by distinct roots. In Pliocene species, the molars became longer, and were more or less coated with cement. The modern horse has extremely long grinders, without true roots, and covered with a thick external layer of cement. The canine teeth were very large in *Orohippus*, and in this genus, as well as those from the Middle Tertiary, appear to have been well developed in both sexes. In later forms, these teeth declined in size, especially as the changes in the limbs afforded other facilities for defence, or escape from danger. The incisors in the early forms were small, and without the characteristic pit of the modern horse. In the genera from the American Eocene and Miocene, the orbit was not enclosed behind by an entire bridge of bone, and this first makes its appearance in this country in Pliocene forms. The depression in front of the orbit, so characteristic of *Anchitherium* and some of the Pliocene genera, is, strange to say, not seen in *Orohippus*, or the later *Miohippus*, and is wanting, likewise, in existing horses. It is an interesting fact that the peculiarly equine features acquired by *Orohippus* are retained persistently throughout the entire series of succeeding forms. Such, e. g., is the form of symphysial part of the lower jaw,

and also the characteristic astragalus, with its narrow, oblique, superior ridges, and its small articular facet for the cuboid.

Such is, in brief, a general outline of the more marked changes that seem to have produced in America the highly specialized modern *Equus* from his diminutive, four-toed predecessor, the Eocene *Orohippus*. The line of descent appears to have been direct, and the remains now known supply every important intermediate form. It is, of course, impossible to say with certainty through which of the three-toed genera of the Pliocene that lived together, the succession came. It is not impossible that the later species, which appear generically identical, are the descendants of more distinct Pliocene types, as the persistent tendency in all the earlier forms was in the same direction. Considering the remarkable development of the group throughout the entire Tertiary period, and its existence even later, it seems very strange that none of the species should have survived, and that we are indebted for our present horse to the old world.

Yale College, New Haven, Feb. 20th, 1874.