Recent polydactyle horses / by O.C. Marsh.

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Recent Polydactyle Horses; by O. C. Marsh.

In this Journal for June, 1879, the writer made a brief summary of the facts then known to him in regard to existing horses with extra digits, especially in relation to the extinct species he had discovered in the Rocky Mountains, and also gave figures of typical examples of existing and fossil forms.* Since then, he has collected much material bearing on the question, particularly of extinct horses, and an illustrated memoir on this subject has long been in preparation. Of recent forms, a number of polydactyle specimens have likewise been secured, some of which show new anatomical points of interest, and are discussed in the present communication.

In the article above cited, various recorded instances of extra digits in the horse are mentioned, some dating back to the beginning of the last century. A much earlier notice is the account of the famous steed of Julius Cæsar, given by Suetonius (*de vita Cæsaris*, LXVI), to which a classical friend has recently called the attention of the writer. According to the historian, Cæsar "used to ride a remarkable horse, which had feet that were almost human, the hoofs being cleft like toes. It was born in his own stables, and as the soothsayers declared that it showed its owner would be lord of the world, he reared it with great care, and was the first to mount it; it would allow no other rider."

It is now known to every one familiar with the modern horse, that the main, functional toe of each foot is the third digit, corresponding to the middle finger of the human hand and foot. In addition to these, two "splint bones," one on each side of the main cannon bone, are present beneath the skin. It is not so well known, however, that the latter are the remnants of two other toes possessed by ancestors of the horse.

* Polydactyle Horses, recent and extinct, this Journal, III, vol. xvii, p. 497, June, 1879; see also by the writer, New Equine Mammals from the Tertiary, Ibid., vol. vii, p. 247, March, 1874; Fossil Horses in America, Am. Naturalist, vol. viii, p. 288, May, 1874; and Introduction and Succession of Vertebrate Life in America, this Journal, vol. xiv, p. 338, November, 1877.

These slender metapodial bones still represent the second and fourth digits, and are shown in their usual position, in figures 1 and 2. One or more of these splint bones may become enlarged below, and support phalanges, forming another digit beside the main one, either beneath the skin, or, more commonly, developing into a small, external toe with hoof.

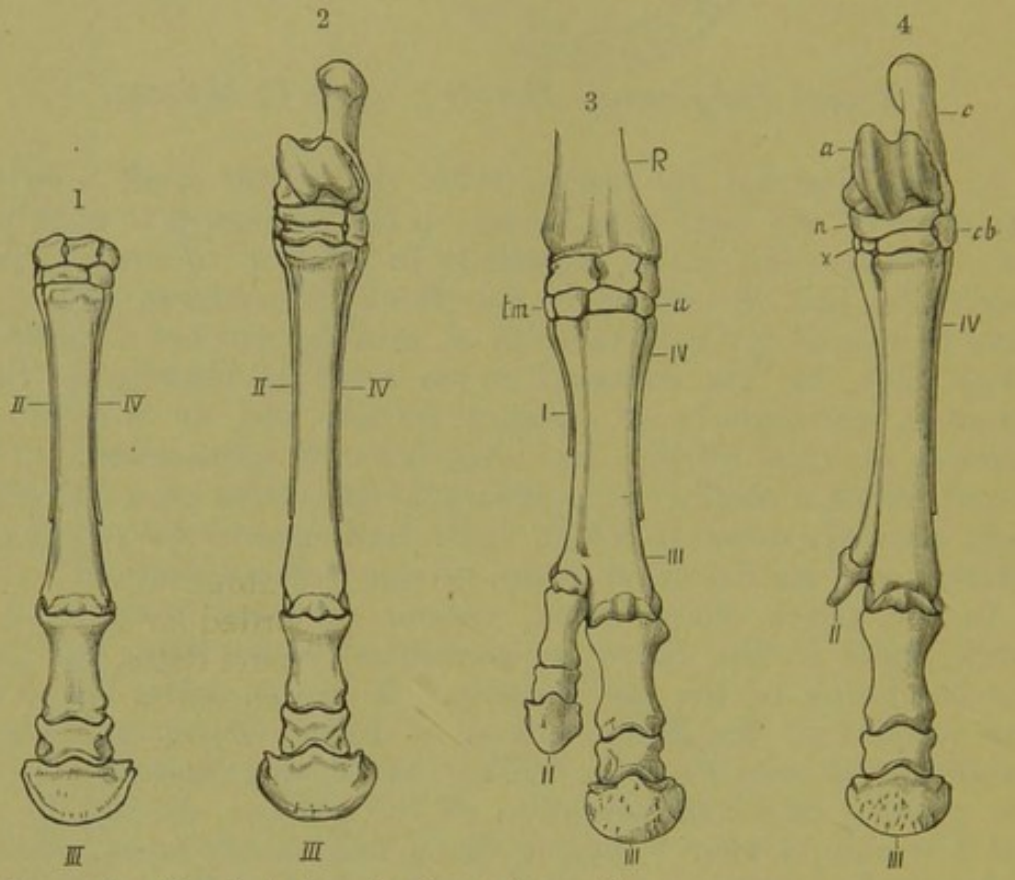

FIGURE 1.—Fore foot of modern horse (normal).
FIGURE 2.—Hind foot of same animal.
FIGURE 3.—Fore foot of "Clique, the horse with six feet" (polydactyle).
FIGURE 4.—Hind foot of same animal. All left feet, and one eighth natural size.

a, astragalus; *c*, calcaneum; *cb*, cuboid; *n*, navicular; *R*, radius; *tm*, trapezium; *u*, unciform; *x*, cuneiform; I. first digit; II. second digit; III. third digit; IV. fourth digit.

The occurrence of such extra digits in the recent horse is much more frequent than is generally supposed. Since the attention of the writer was first called to the subject, he has seen and examined a large number of living animals with this peculiarity, and has had sent to him several interesting specimens of the same character. He has likewise received photographs, drawings, and detailed descriptions of various other examples, the authenticity of which cannot be questioned. This material, together with not a few published accounts, forms a fair basis on which to investigate the subject. This, however, would require much time in itself, especially if it led into the question whether polydactylism is atavism, and other

allied topics. In the present paper, it is intended merely to state the more important facts, and what they indicate, leaving the full discussion for another occasion.

The cases of supernumerary digits in the existing horse now known to the writer may be roughly classified, as follows:

(1) An extra digit on one foot. This is always much smaller than the main, or third, digit, the largest seen being about one half its size, and the smallest, very diminutive. This extra toe is almost invariably on the inner side of the main digit, and usually on the fore foot. Not infrequently it may be entirely beneath the skin, the only external evidence of it being a prominence, which, on close examination, will often be found to contain, below the splint bone, two or more movable phalanges, but sometimes only a single one, and very small.

(2) A corresponding extra toe may be present on the other fore foot, equally developed with the opposite one, but occasionally much smaller, or even concealed under the skin.

(3) A second extra digit may exist with those above described, but outside the main digit. This toe, as a rule, is smaller than the inner one, but may equal or exceed it.

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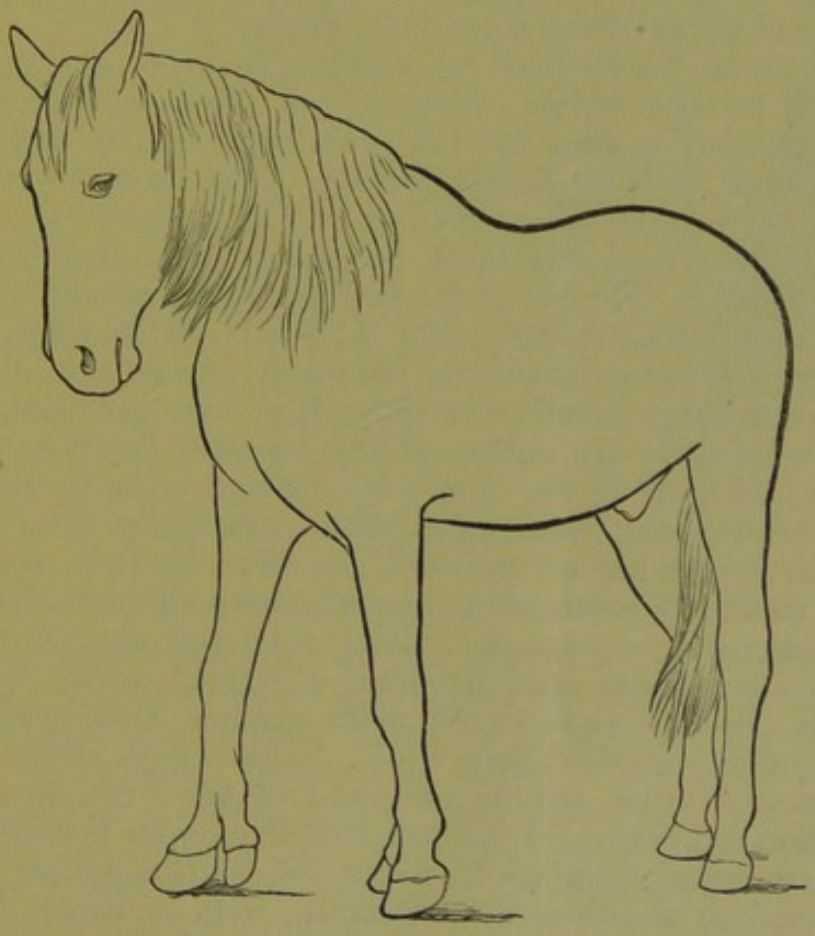

FIGURE 5.—"Clique, the horse with six feet," showing two extra digits.

(4) With the extra inner toes of the fore feet, another of equal or smaller size may be present on one or both of the hind feet, almost always on the inside. Usually, however, these posterior toes are much smaller, and often beneath the skin, when the anterior extra digits are well developed. An example of the equal development of all the inner toes, fore and aft, is shown below in figure 6, which represents an animal examined during life, by the writer. Occasionally the hind feet may each have two extra digits, while the fore feet have only one, as in the horse shown in figure 7.

(5) In rare cases, both fore and hind feet may each have two extra digits fairly developed, and all of nearly equal size, thus corresponding to the feet of the extinct *Protohippus*, which are represented in the diagram on page 355.

(6) Sometimes, besides the extra toes above described (which appear to be always the second and fourth), the first digit, or pollex, may be represented by its metacarpal, supported by a distinct trapezium, all beneath the skin. In such cases, the fifth digit, corresponding to the little finger of the human hand, alone is wanting. Three examples of this four-toed polydactylism are preserved in the Yale Museum, and one of them is shown in figure 3. This type is of special importance, and is described more fully below.

The horse which best represents this type was examined casually by the writer when it was alive, and at its death was presented to him for the Yale Museum by the owner, Theodore F. Wood, of New Jersey. The animal was widely known to the general public as "Clique, the horse with six feet," having been exhibited for many years, in this country and in Europe. He was said to be from Texas, and at his death, in January, 1891, was very old. This horse, when alive, showed an extra digit of good size on the inside of each fore foot, and a corresponding prominence on each of the hind feet, but no free lateral toe. An outline of this horse is shown in figure 5.

The first digit of the fore foot, corresponding to the thumb of the human hand, was not apparent externally, but, by close examination, could be detected beneath the skin, where the upper part of the splint bone appeared as a ridge. The second digit was the free extra toe, which attracted especial attention from its large size, and pendent, elongated hoof. Its metatarsal is closely united to the main cannon bone, which thus seems much broader than usual. The fourth digit appears only as the usual splint bone, and of the fifth, there is no indication whatever. The hind feet showed no peculiarity except the inner prominence above the fetlock, formed by the lower end of the second metatarsal, with a single movable

phalanx and its sesamoid. In other respects, the limbs were well shaped, and in fair condition for so old a horse.

After the death of the animal, a careful dissection of the feet was made, and several points of interest became apparent. First of all, in the fore feet, the presence of the first digit was demonstrated by a robust, splint metacarpal about half the length of the main cannon bone. This splint was supported above by a large trapezium having the usual articulations of that bone in its full development. The first digit, as present in the left foot of this horse, is shown above in figure 3. In the opposite fore foot, this digit is also represented, and equally developed, as seen in figure 8.

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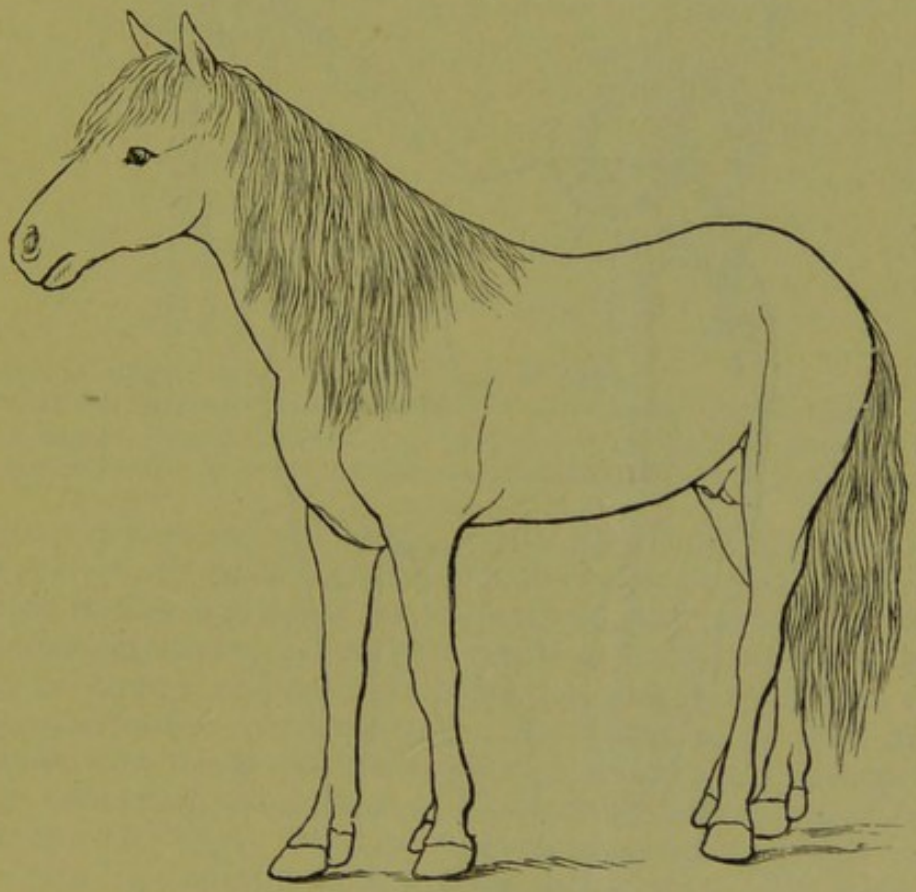

FIGURE 6.—"Eight-footed Cuban horse," with extra digit on each foot.

The second metacarpal of the left fore foot is quite large, and fully developed above and below, but its shaft is coössified with the main metacarpal. The line of the suture uniting the two is still strongly marked, as shown also in figure 3. The phalanges and sesamoids are all well developed, and had this toe been long enough to reach the ground, it would have afforded a strong lateral support to the main digit. The latter possesses no marked peculiarities except that the outer side is

more developed, especially in the coffin bone. The fourth digit is represented by a strong splint bone similar to that in the normal foot of the existing horse. The opposite fore foot appears to correspond in all respects with the one here described and figured.

The hind feet of this animal present some further points of importance. The first digit is wanting, but the first cuneiform bone is present, and well developed.* The second digit is represented by a strong, complete metatarsal, coössified along its main shaft with the large cannon bone of the third digit, but with both extremities free. It was supported above by

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FIGURE 7.—"Horned horse from Texas," showing six extra digits.

*The name cuneiform as applied to the ulnare bone of the carpus is misleading, and should be discontinued, as the same word is used for two or more bones in the second row of the tarsus. The name pyramidal employed by many anatomists is not open to this objection, and its use for the ulnare is to be recommended.

two united cuneiform bones. The lower extremity of this metatarsal carried a single phalanx, with a posterior sesamoid evidently formed of two bones. The main cannon bone and its phalanges show no marked peculiarities except some obliquity. The fourth digit is represented by a large splint metatarsal, as shown in figure 4. The opposite hind foot appears to be similar in all respects, except that the three small cuneiform bones are separate, as shown in figure 9.

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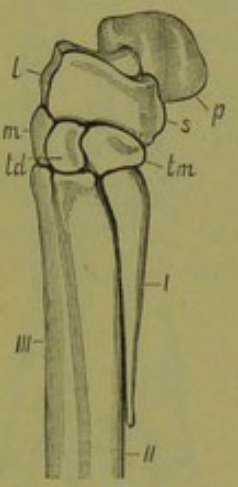

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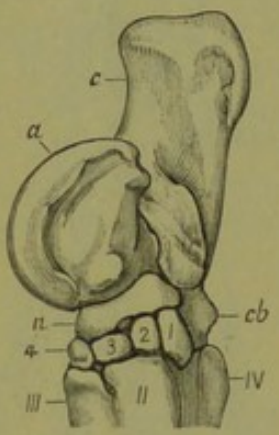


FIGURE 8.—Right carpals and metacarpals of "Clique."
FIGURE 9.—Right tarsals and metatarsals of same animal. One fourth natural size.
a, astragalus; *c*, calcaneum; *cb*, cuboid; 1, 2, 3, 4, cuneiform bones; *l*, lunar; *m*, magnum; *n*, navicular; *p*, pisiform; *s*, scaphoid; *td*, trapezoid; *tm*, trapezium.

In no case examined by the writer has there been conclusive evidence of any extra digit except one of a true pentadactyle foot, such as is now known in the ancestry of the horse. In every specimen examined, where the carpal or tarsal series of bones were preserved, and open to inspection, the extra digits were supported in the usual manner. No instances of true digital division were observed, although such cases might be expected. It is noteworthy that none of the extra toes examined represents the fifth digit, although the reappearance of this rather than the first might naturally be looked for. No digit has been noticed with more than three phalanges.

A large majority of the polydactyle horses known to the writer in this country, have been raised in the Southwest, or from ancestry bred there, so that their connection with the Mustangs or semi-wild stock of that region becomes more than probable. It is well known that the tendency to reversion is much stronger where animals run wild, and this fact must be taken into consideration in discussing the present question, for the late ancestors of the Mustang were certainly wild for at least several hundred years.

No example of extra digits has been observed by the writer in any wild species of existing equine mammals of the old world, or their immediate descendants, although it is evident that such cases are probable, and careful observation would doubtless bring them to light, especially if made in the native haunts of those animals.

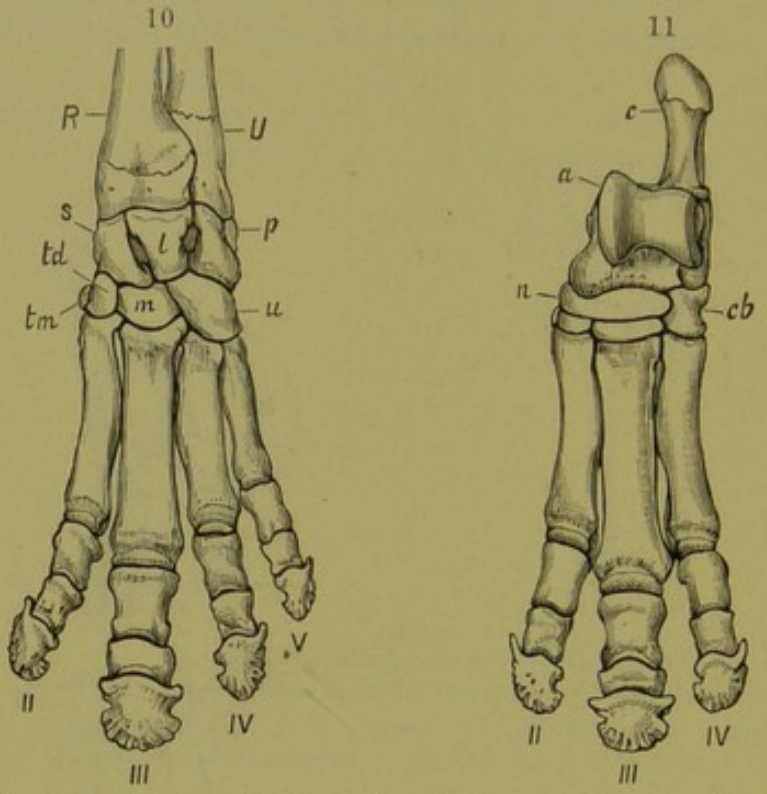


FIGURE 10.—Left fore foot of recent Tapir (*Tapirus indicus*, Cuvier).
FIGURE 11.—Left hind foot of same animal. One fifth natural size.

Many examples of polydactyle feet in the recent horse, preserved in museums, have been cut off below the carpus or tarsus, and thus the real significance of the extra digits has been lost. The whole carpal and tarsal series, and the distal ends, at least, of the bones above them, may be important elements in the problem to be solved, if reversion or atavism is to be considered.

In reviewing what is now known of the extra digits in the existing horse, a few points are manifest, which could not have been anticipated from previous knowledge of the perissodactyle foot:

(1) The presence of a first digit in the fore foot, represented by a strong, styliform metacarpal supported by a well-developed trapezium, with its usual articulation, in the same foot in which the fifth digit is wanting.

(2) The frequent appearance of the second digit as a distinct, free toe in one or more feet, and the large size it attains, while the other digits, except the third, are aborted or wanting.

(3) The presence of five distinct bones in the second row of the tarsus. One of these is the cuboid fully developed; next, the external cuneiform bone supporting the great metatarsal; then three smaller bones on the tibial side. These five tarsals correspond either to those in the reptilian foot, or the first may be regarded as a sesamoid, and the cuboid, as double (including the fourth and fifth), as it is now usually considered by anatomists. Another explanation may be suggested; namely, that the inner, pendent bone is a remnant of the first metatarsal. Such a rudiment apparently exists in some fossil horses, and its appearance in the hind foot of a recent animal which had the first digit of the fore foot so well represented would not be strange. The bone usually regarded as the inner cuneiform in the existing tapir and rhinoceros may, perhaps, include the same remnant. In the modern horse, this bone is sometimes double, but the specimen represented in figure 9 shows that it may be composed of three elements.

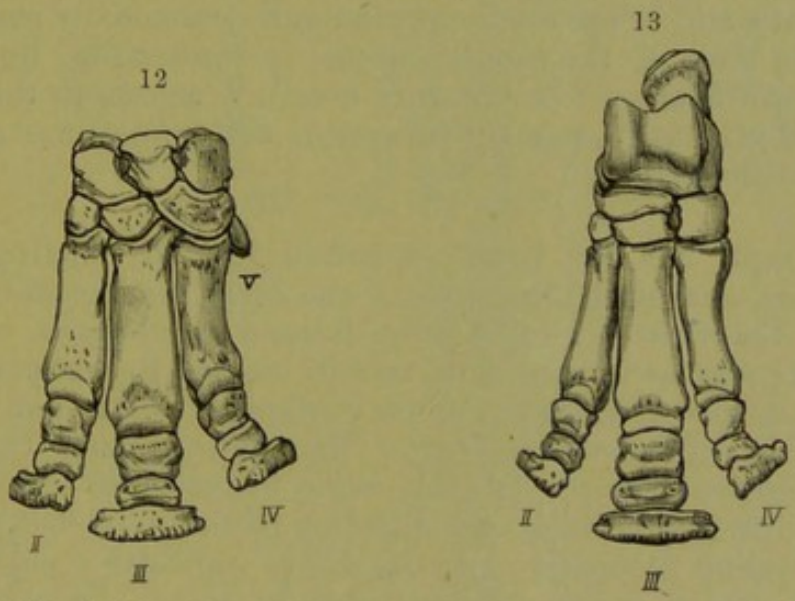


FIGURE 12.—Left fore foot of *Rhinoceros bicornis*, Linnæus.
FIGURE 13.—Left hind foot of same animal. One eighth natural size.

The frequent reappearance of the second digit as an extra toe in the modern horse would seem to indicate that this feature was functional in a late ancestor, but no fossil equine with two toes has yet been found.*

The presence of four toes in the fore feet, each supported by its true carpal bone, is a fact of much importance, and is clearly a case of reversion. The four distinct cuneiform bones

* A small species of *Pliohippus* from the Pliocene of Oregon may be an exception. An incomplete hind foot in the Yale Museum shows the second metatarsal as a splint bone, the third very long and slender, and the fourth so well developed that it probably supported phalanges. This may also be a case of reversion. The species is new, and may be called *Pliohippus gracilis*.

in the hind foot of the same animal offer another point of interest, especially in connection with the corresponding carpal series.

The hoofs of the extra digits of the modern horse vary much in size and form at birth, and are subsequently affected by the surroundings of the animal, and the care it receives. If these hooflets are low enough to reach the ground, their growth is checked by wear, like the large hoof, although in less degree. As the main hoofs will become of abnormal length, and more or less twisted, if the animal is confined to soft, boggy ground, so the extra hoofs having no wear, and receiving no pruning, often become much elongated and curved, or by trimming may assume the form of a spur or horn. The "horned horse from Texas," shown in outline in figure 7, probably received some attention of this kind, as the hooflets are much more pointed than any examined personally by the writer.

The cleft seen in the last phalanges, or hoof bones, of *Orohippus* and other fossil equines, and occasionally present in the coffin bone of the modern horse, is interesting, but of no special significance. It certainly does not represent the union of two digits, as frequently supposed, and sometimes asserted by scientific writers.

The tapir has the most primitive feet of existing perissodactyles, and most like those of the early predecessors of the horse. The feet of the Middle Eocene *Orohippus* were, in fact, very similar in structure, as will be seen by comparing the manus and pes of each as shown in figures 10–11, and 16–17. The living rhinoceros has feet of the same general type, but less primitive (figures 12–13), while the modern horse, when normal, has the extreme specialization of the monodactyle foot. The frequent reversion to extra digits indicates a polydactyle ancestry, which is now demonstrated by actual discovery.

The terms *Perissodactyla* (odd-toed) and *Artiodactyla* (even-toed) proposed by Owen, and now in general use to distinguish two great groups of hoofed mammals, are misleading, and a stumbling block to the lay reader, as well as to many popular writers on science. The horse, tapir, and rhinoceros are the only recent examples of the so-called perissodactyles, or odd-toed ungulates, and the pig and peccary are certainly typical artiodactyles. The tapir, however, has four toes in the front foot, while the peccary has three only behind, and these exceptions do not prove the rule, for the number of toes alone has nothing to do with the profound distinctions separating the two groups, at least in all recent forms.

In the horse and its allies, recent and extinct, the axis of each foot passes through the middle of the main, or third, digit, while in all the so-called even-toed mammals, the axis is always along the side of this digit. This is the essential difference between the feet of the two groups.

The names *Mesaxonia* (middle axis) and *Paraxonia* (side axis) proposed by the writer in 1879,* as substitutes for Owen's terms, are more exact definitions, but thus far have not met with general favor, for it seems almost impossible to dislodge an established error in science. The term "coral insect," for example, of the older writers, still maintains its place in popular science, and even in some modern text books.

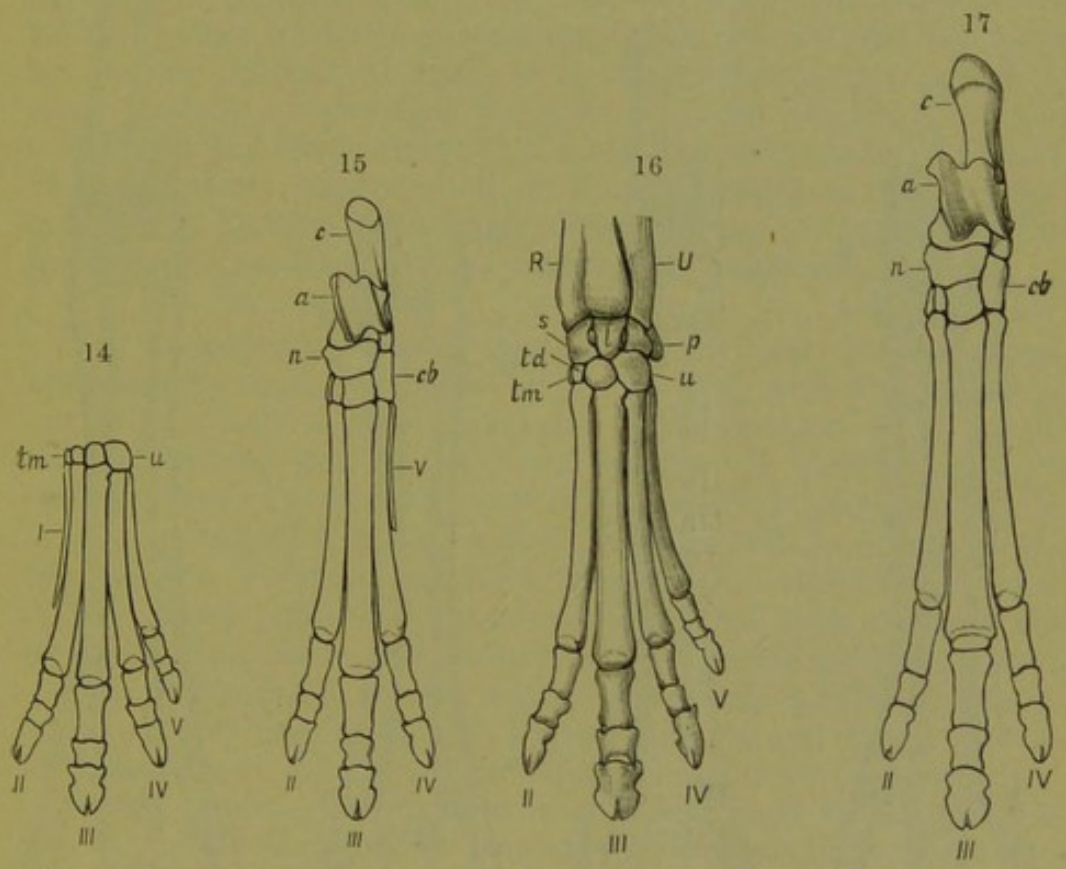


FIGURE 14.—Fore foot of oldest fossil horse, *Eohippus pernix*, Marsh.
FIGURE 15.—Hind foot of same. Lower Eocene.
FIGURE 16.—Fore foot of *Orohippus agilis*, Marsh (type).
FIGURE 17.—Hind foot of same. Middle Eocene. All left feet, one half natural size.

In explanation of the extra digits of the recent horse, two views have been advanced: (1) that they are reduplications of the main digit, like the occasional sixth finger of the human hand, or result simply from a division of this toe; (2) that they are true cases of reversion to a polydactyle ancestor. The former view was long held by writers on the subject, and

* This Journal, vol. xvii, p. 501, June, 1879.

is still maintained essentially by some eminent anatomists.* The large number of cases, however, now investigated by the writer make it probable that, for most instances, at least, the second explanation is the true one.

In the case of horses, recent and extinct, the question of atavism is much simplified, as they start with a pentadactyle form, and each successive change in the modifications of the limbs, and of the feet, and likewise in the dentition, can be traced through a regular series from the early Tertiary down to the present time. Nearly every instance of polydactylism

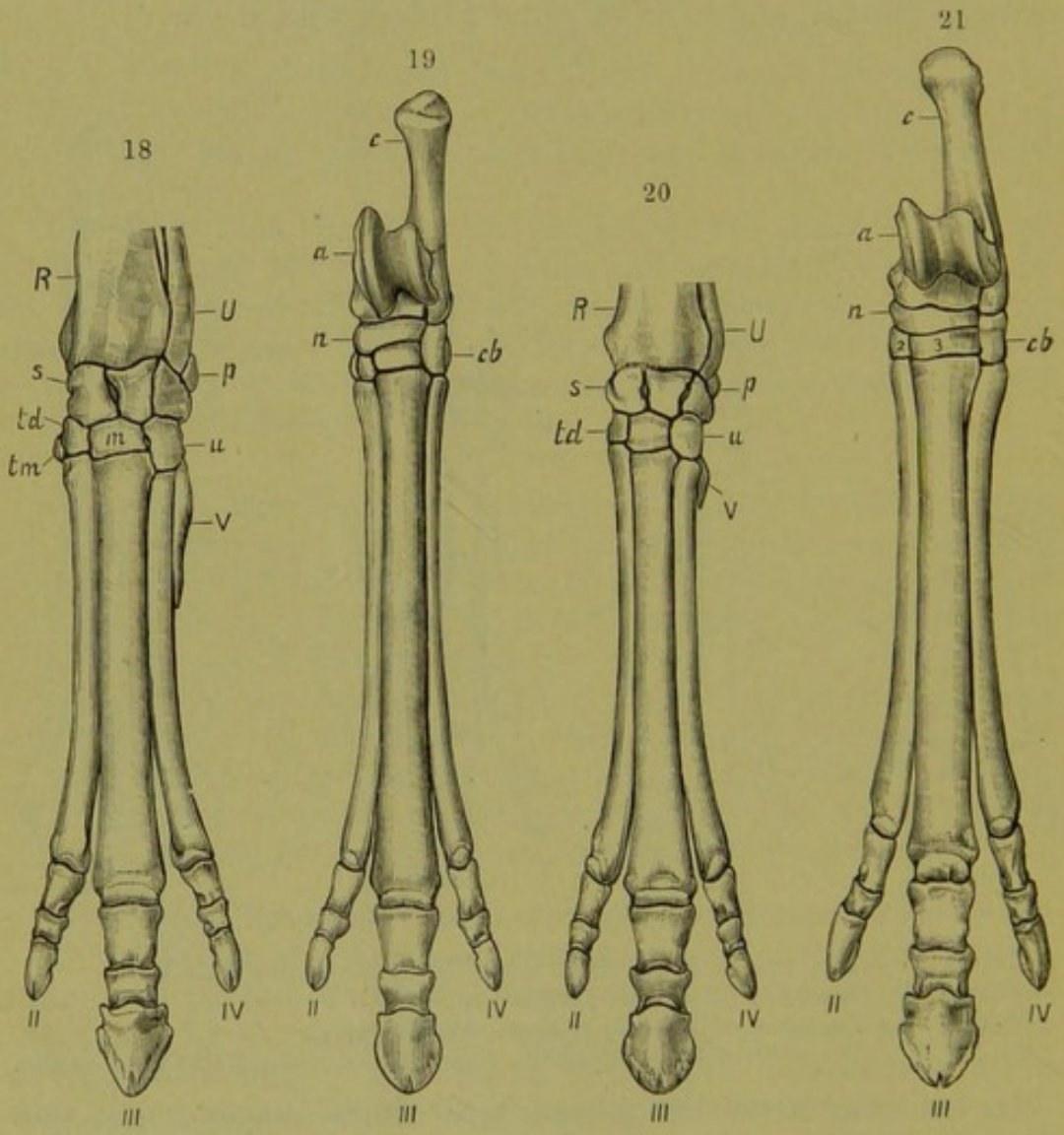


FIGURE 18.—Left fore foot of *Mesohippus celer*, Marsh.
FIGURE 19.—Left hind foot of same. One half natural size. Lower Miocene.
FIGURE 20.—Left fore foot of *Miohippus anceps*, Marsh.
FIGURE 21.—Left hind foot of same. One third natural size. Upper Miocene.

* Flower, Osteology of the Mammalia, p. 296, 1885; and Gegenbaur, Morphologisches Jahrbuch, p. 584, 1880.

observed in the modern horse has its counterpart in some extinct species now known, and it is not at all improbable that future discoveries will bring to light examples corresponding to the present apparent exceptions.

All the examples of polydactylism in the horse which the writer has had opportunity to examine critically are best explained by atavism, and many of them admit no other solution. Taken together with the fact now known of their great frequency, they clearly indicate the descent of the horse from comparatively recent polydactyle ancestry.

The writer has traced back the genealogy of the horse through various stages, to a form, *Eohippus*, in which all five toes were represented, and has likewise given an explanation of the change which in succeeding forms has reduced the number to one functional digit, as in the existing horse. It is in these extinct species that the true solution of the problems relating to the extra digits of the modern horse is to be sought. In the various papers cited at the beginning of the present article will be found the main facts relating to the ancestry of the horse as made out by the writer from American forms.

The oldest ancestor of the horse, as yet undiscovered, undoubtedly had five toes on each foot, and probably was not larger than a rabbit, perhaps much smaller. This hypothetical predecessor of the horse can now be predicated with certainty from what is known of the early hoofed mammals. It may be called *Hippops*, and its remains will be found at the base of the Tertiary, or more likely in the latest Cretaceous. A still more primitive ancestral form, and next older in the series of Ungulates, will show the more generalized characters of the group called by the writer *Holodactyla* (Dinocerata, p. 172), from which both the Perissodactyles and the Artiodactyles branched off before the equine line became distinct.

It is impossible to say from what generalized form the horse line first separated, but at present the probabilities point to a genus allied to the Eocene *Hyracotherium*, Owen (1839), as the stem. In the latter genus, the molar teeth are of the bunodont type, the tubercles being conical and distinct. Similar teeth are characteristic of suilline mammals, and from the teeth alone, the two groups could not be distinguished, but it is now probable that the latter appeared as a distinct group later than the equine mammals, and that their oldest representatives were very diminutive in size.

The American representative of *Hyracotherium* was first described by the writer under the name *Helohyus*,* and another form, nearly allied, as *Thinotherium*, all three being

* This Journal, vol. iv, pp. 207, 208, September, 1872.

at first supposed to have close affinities with suilline mammals. Some of the latter may, in fact, be included in the species referred to these genera. Various perissodactyle forms, also from the Eocene of this country, have since been described by Cope under the generic name *Phenacodus* (1873), which is clearly identical with *Helohyus*, and some of these have been referred, under the former name, to the equine ancestral line.* These mammals have been placed by the writer in a distinct family, the *Helohyidæ*.†

Helohyidæ.

The *Helohyidæ* may with some probability be now regarded as the family from which equine mammals were derived. The members of this group were small perissodactyle mammals, with forty-four teeth without cement, the premolars unlike the molars, and both with short bunodont crowns. The ulna and fibula were complete and separate, and the feet had four or five functional digits. All the known forms are from the Eocene. During Tertiary time, this family apparently separated into various branches, some of which became specialized, and died out, while smaller forms became modified into the lines by which the horse, the tapir, and the rhinoceros gradually developed.

Orohippidæ.

The successors along the first line form a well-marked family, which the writer has called the *Orohippidæ*.‡ The representatives of this group were small equine mammals having forty-four teeth without cement, incisors without pit, canine teeth large, and the molar series with short crowns, and the cusps more or less flattened. The ulna and fibula were complete, and there were three or four functional digits in each foot. The members of this family appear to be all from the Eocene or Miocene.

Equidæ.

Next in the succession came the *Equidæ*, of which the horse is a typical member. All are large equine mammals, with less than forty-four functional teeth with cement, incisors with pit, canines small or wanting, the molars elongated, and the premolars essentially like the molars. The ulna and fibula are incomplete, and there is but one functional toe on each foot. These mammals lived in Pliocene time, continued on to the present, and are now represented by the horse, ass, zebra, and quagga.

* W. H. Flower. The Horse, London, 1891; also, Madame Pavlow, L'Histoire Pal. des Ongules, I–V, Moscou. 1887–1890.

† This Journal, vol. xiv, p. 364, November, 1877.

‡ Ibid., vol. vii, p. 249, 1874.

The dividing lines between these three families are not sharply defined, and cannot be, if evolution is true; in fact, the divisions in all classifications of extinct animals are, of necessity, like the book shelves in a library, merely convenient stages for the arrangement of present limited knowledge.

Among the extinct equines known in this country, the first genus of the series is *Eohippus*, described by the writer from the Coryphodon beds at the base of the Eocene (this Journal, vol. xii, p. 401, 1876). This is the oldest and most diminutive form, being about the size of a small fox. There is a diastema between the canine and first premolar, but none between the premolars, which are all unlike the molars. Three species are known. The feet of one species are shown in figures 14 and 15, and those of the others so far as known are similar.

In the next higher horizon of the Eocene, remains of another small equine mammal are found, which may be placed in a new genus, *Helohippus*. The type specimen was described by the writer in 1871, as *Lophiodon pumilus* (this Journal, vol. ii, p. 38), and others have since been found in the same horizon. This genus has a diastema between the first and second premolars, and the last premolar is like the molars. The known representatives of *Helohippus* are about as large as a fox.

The next genus in the series is *Orohippus*, described by the writer from the Dinoceras beds of the Middle Eocene (this Journal, vol. iv, p. 207, 1872). This form is the type of the family *Orohippidæ*, and almost every part of the structure of several species is now known. The best preserved specimens show that there is no diastema between the upper premolars, and the third and fourth are similar to the molars. The skull is elongate, and has no antorbital fossa. The fore and hind feet of one species are shown in figures 16 and 17. Several other species are known, all about the size of a fox.

Another allied genus, *Epihippus*, occurs in the Diplacodon beds of the Upper Eocene. This genus, proposed by the writer in 1878 (Proc. Am. Assoc. Adv. Sci., page 236), also shows no diastema between the first and second premolars above or below, and the third and fourth are essentially like the molars. Two species are known, both somewhat larger than those of *Orohippus*, but having the same general structure, although the dentition and feet differ in several respects, being intermediate between that genus and the following.

At the base of the Miocene, in the Brontotherium beds, another equine mammal is comparatively abundant, and has been referred by the writer to a distinct genus, *Mesohippus* (this Journal, vol. ix, p. 248, 1875). The two species known are about as large as a sheep, and the feet of one are shown in

figures 18 and 19. The ulna is complete, but the fibula is not. There is no diastema between the premolars, and the third, fourth, and fifth are like the molars.

In the Upper Miocene of Oregon, the series is continued in *Miohippus*, a genus established by the writer in 1874 for several species found in this formation (this Journal, vol. vii, p. 249). All are much larger than *Mesohippus*, and more specialized in the skull and feet. The latter are shown in figures 20 and 21. The premolars form a continuous series, and three of them are of the molar type. This genus appears to be the American representative of *Anchitherium*, von Meyer (1844), but is somewhat less specialized.

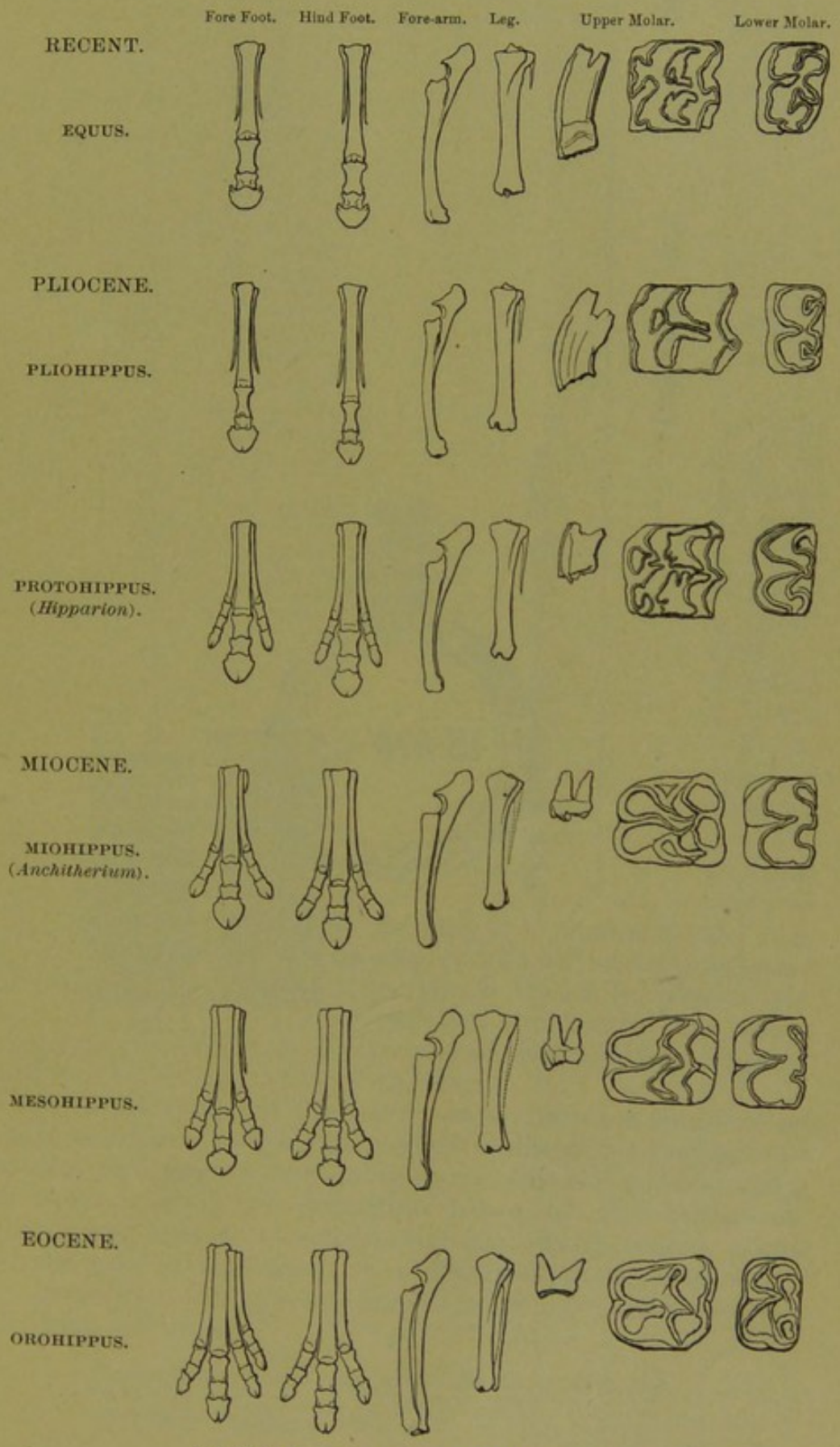
In the early Pliocene of this country, the genus *Protohippus* of Leidy (1858) is especially abundant, and several species about as large as a donkey are known. All have three functional toes on each foot, but these are more nearly of a size than the digits of the European *Hipparion* of Christol (1832). In the later deposits of this formation, three-toed horses are replaced by *Pliohippus*, named by the writer in 1874 (this Journal, vol. vii, p. 252). This genus has many species, all smaller than the horse, but with similar feet. A true *Equus* is entombed in a higher horizon, but apparently became extinct before America was discovered.

The type specimens of all the genera of fossil horses proposed by the writer up to 1876 were carefully studied by Prof. Huxley in that year, and made the basis of one of his New York lectures.* The diagram shown on page 355 was prepared for that lecture under his direction, from specimens in the Yale Museum collected and described by the writer. It gives the main characters of the genera, and represents clearly the evolution of the horse as then determined from American specimens.

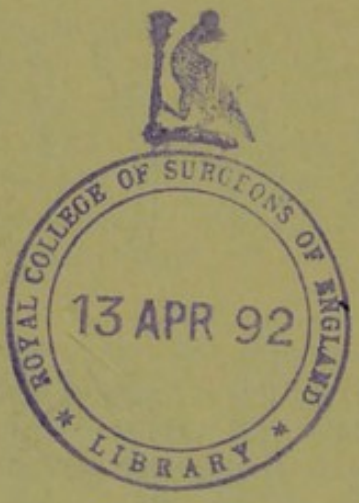
Since then, the writer has made large collections of remains of these and other genera and species, and the whole forms by far the largest series ever brought together. An examination of this collection makes still more evident the line of equine descent on this continent, and the genera since named, and described (*Eohippus*, *Helohippus*, and *Epihippus*), help to complete the series. Many details are yet wanting, but the writer hopes at an early day to bring all the facts together, and make out as far as possible the genealogy of the horse.

New Haven, Conn., March 24th, 1892.

* American Addresses, p. 88, London, 1877.



GENEALOGY OF THE HORSE.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