Ocean; for, if the transportation of the pebbles and sand was really due to the tide, it would indicate the existence of an Atlantic basin in pre-palæozoic days, from which the forced wave flowed over or through these successive reefs or ledges into the midland basin.

THE PERISSODACTYLA.

BY E. D. COPE.

(Concluded from page 1007.)

THE CHALICOTHERIIDÆ had numerous representatives during Eocene time, and a few species of Chalicotherium extended into Miocene time. The boundaries which separate the family from the Lophiodontidæ on the one hand and the Menodontidæ on the other are not always easy to determine. From the former the symmetrically-developed external V's of the superior molars and the double V's of the inferior molars distinguish it; yet in Pachynolophus the anterior cingular cusp produces a part of the

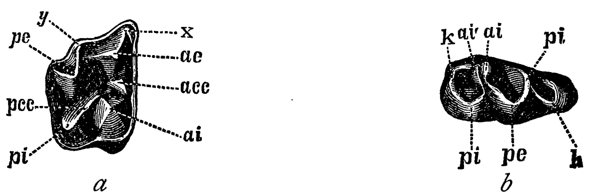
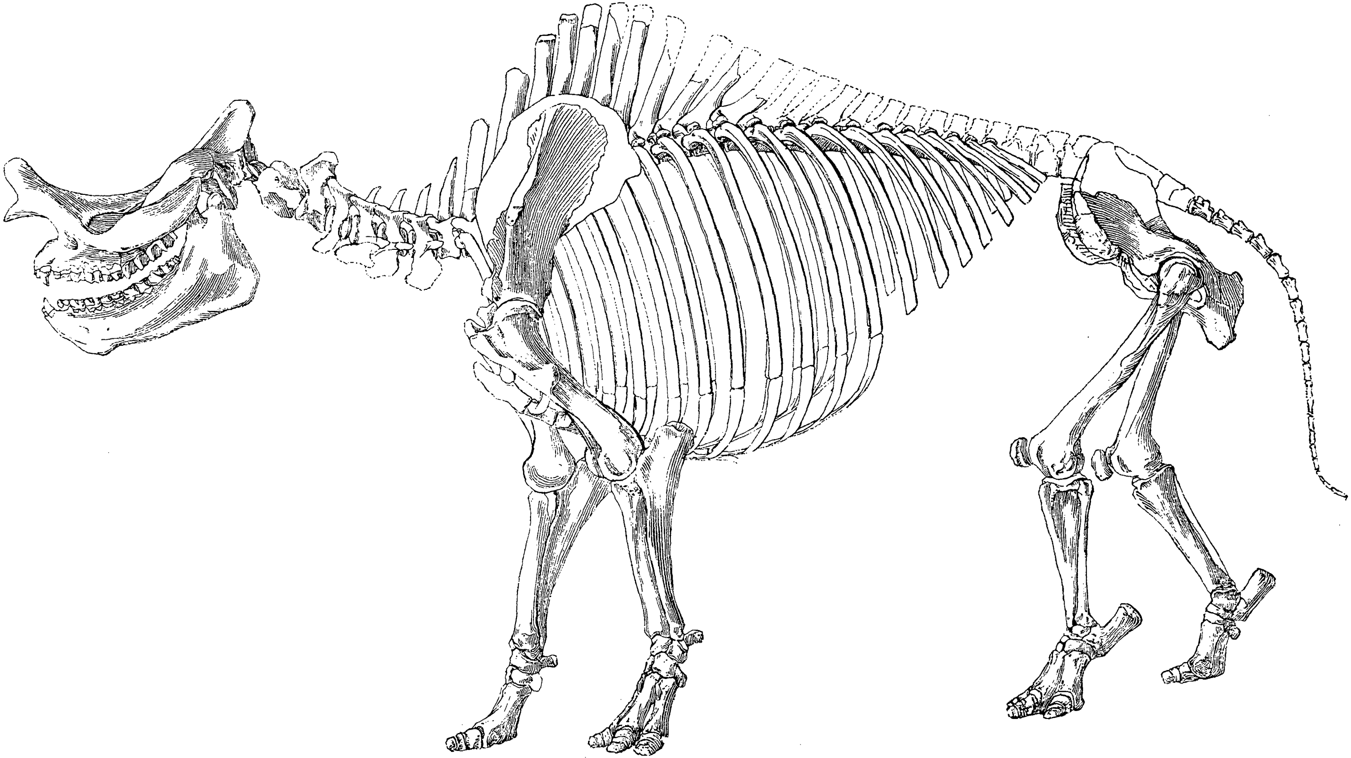


FIG. 24. *Lambdotherium popoagicum* Cope, molar teeth, natural size; from Wind River Eocene of Wyoming. From Wortman, after Cope. Fig. *a*, second superior molar; *b*, last inferior molar. *ae* and *pe*, anterior and posterior external V's; *y*, intermediate external rib; *x*, anterior external angle; *pi* and *ai*, anterior and posterior internal tubercles; *acc* and *pcc*, anterior and posterior intermediate tubercles; *h*, heel.

asymmetry found in the Lophiodontidæ. The character of the double inner cusps of the superior premolars, which distinguishes the Menodontidæ, is only found in the last premolar in Diplacodon of the latter, while a trace of the additional cusp of this tooth is found in the Chalicotheroid Nestoritherium.

In using the following table it must be borne in mind that the structure of the feet has not been determined in several of the genera:

PLATE XXXII.



Menodus giganteus Leidy, one twenty-fourth natural size; from White River (Oligocene) bed of Nebraska. From Scott and Osborn, in Bulletin Mus. Compar. Zoölogy, Cambridge, Mass.

I. Internal cones of superior molars separate from external lobes.

A. External tubercles subconic, separated by a vertical external tubercle.

Fourth inferior premolar like first true molar;.................*Ectocium* Cope.

Third and fourth inferior premolars like the true molars;...*Epihippus* Marsh.[1]

AA. External tubercles of superior molars become V's, which are separated externally by a vertical ridge.

a. Incisors present.

β. No diastema in front of second inferior premolar.

Second premolar without inner lobe; last molar with one inner cone;..*Leurocephalus* S. & O.

Second premolar with inner cone; last superior molar with an inner cone;..*Palæosyops* Leidy.

Second premolar with inner cone; last superior molar with two inner cones; ....*Limnohyus* Leidy.

ββ. A diastema in front of second inferior premolar.

Two inner cones of last superior molar;........................*Lambdotherium* Cope.

aa. Incisors absent from both jaws.

Last superior molar with one internal cone;...................*Nestoritherium* Kaup.

II. One or both internal cusps of superior molars united with the external lobes by cross-crests.

a. External cusps of superior molars more or less conic.

An antero-external cingular cusp;................................*Pachynolophus* Pomel.

aa. External lobes of superior molars, inflected V's.

β. No crescentic inner lobes.

Intermediate lobes confluent;...*Chalicotherium* Kaup.

FIG. 25. *Ectocium osbornianum* Cope, molars, natural size; from the Suessonian of Wyoming. Fig. *a*, superior molars; *b*, inferior molars. Original.

FIG. 26. *Lambdotherium popoagicum* Cope, lower jaw ramus, natural size; from Wind River Eocene of Wyoming. Original.

The phylogeny of this family is not difficult to read. Ectocium, if it be truly a member of it (the feet are unknown), is clearly the primitive genus, which is not far removed from Systemodon of the Lophidontidæ, in characters. The flattening of its external cusps produced the two external V's of the other genera, and this, without further modification, would give us Leurocephalus and Palæosyops, the former having the second superior premolars more simple than in the latter. This type,

[1] Teste Scott and Osborn.

with diastemata, is Lambdotherium. The same type, without incisors, gives us the Asiatic Nestoritherium. The development

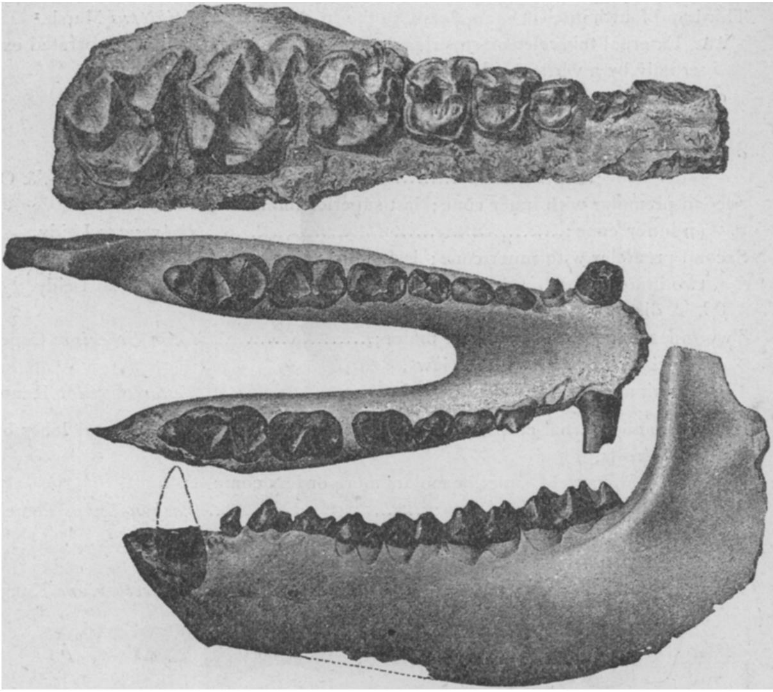


FIG. 27. *Palæosyops major* Leidy, superior molar teeth, one-half natural size; after Cope. From the Bridger Eocene of Wyoming.

of cross-crests is accomplished, as in other families, by the compression and fusion of the intermediate and internal tubercles. When the external V's are little pronounced, we have Pachynolophus; when they are well developed and the anterior inner tubercle remains distinct, we have the genus Chalicotherium. These relations are probably phylogenetic, and may be represented as follows:

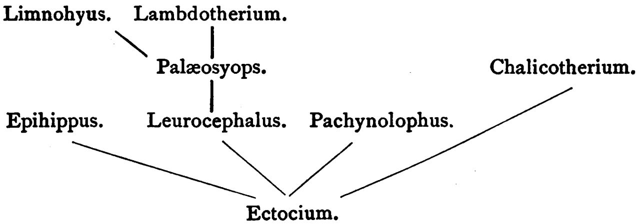
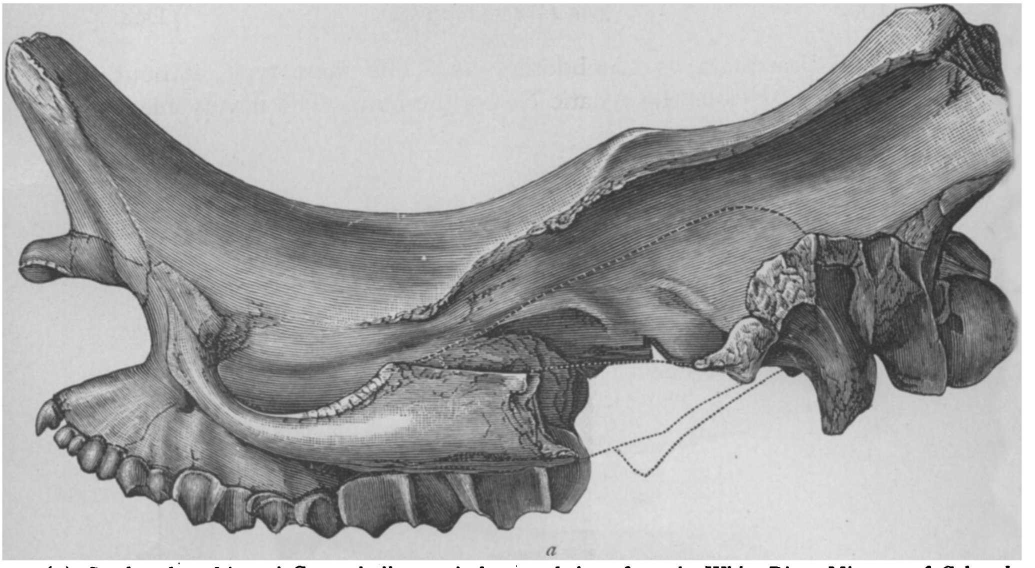
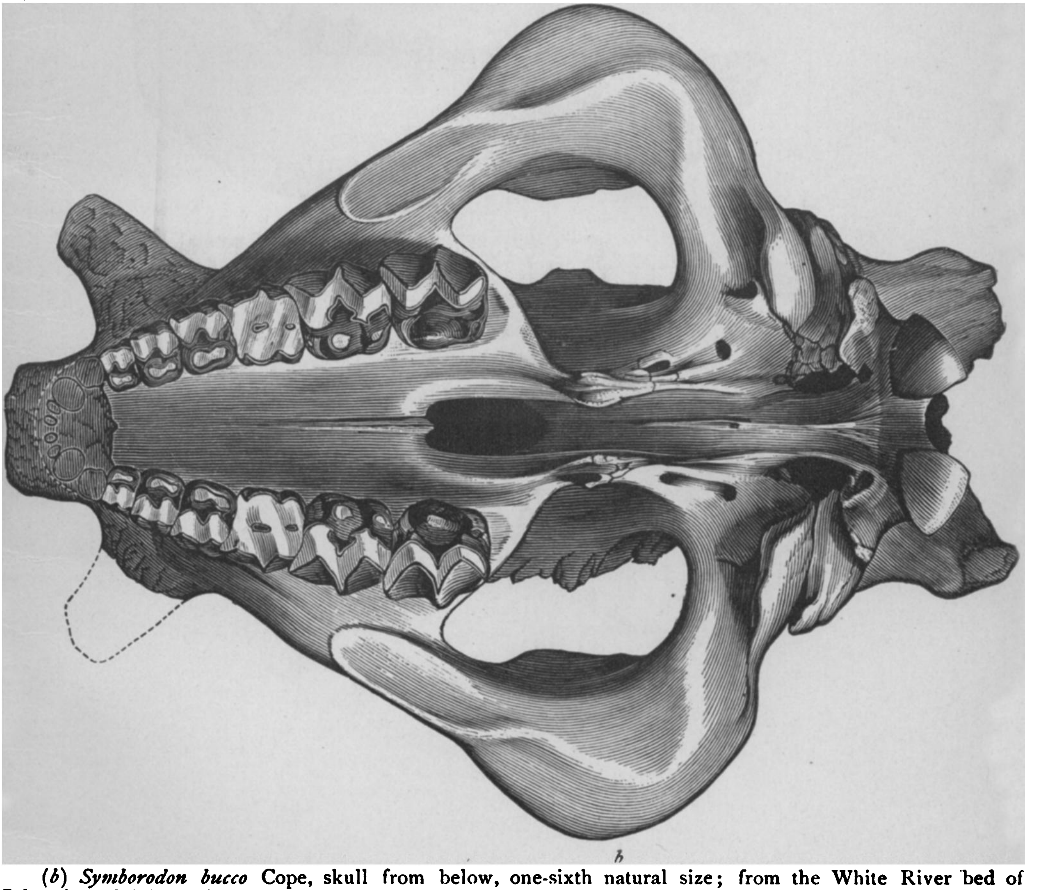


PLATE XXXIII.



(*a*) *Symborodon altirostris* Cope, skull, one-sixth natural size; from the White River Miocene of Colorado Original; from Ann. Report U. S. Geol. Surv. Terrs., 1873.



(*b*) *Symborodon bucco* Cope, skull from below, one-sixth natural size; from the White River bed of Colorado. Original; from Ann. Report U. S. Geol. Surv. Terrs., 1873.

The known genera of MENODONTIDÆ are all American. They differ as follows:

a. Last superior premolar only with two inner tubercles.
Incisors present; no horns on the muzzle;..............................*Diplacodon* Marsh.
aa. All the superior premolars with two interior cusps.
Six inferior incisors; canines very large;..............................*Dæodon* Cope.
Six inferior incisors; canines very small; horns on the muzzle;...*Menodus* Pomel.
No inferior, and four small superior incisors; canine very small;
horns on the muzzle;...*Symborodon* Cope.

Diplacodon, in its simpler premolars, approaches the Chalicotheriidæ, and is the oldest of the American genera. It is from the Diplacodon bed or Upper Eocene. Menodus and Symborodon, which include some species of gigantic size, belong in the White River or Oligocene, while Dæodon has, so far, only been obtained from the John Day or Middle Miocene. The phylogeny of the family is simple, as Diplacodon is clearly the ancestor of Dæodon on the one hand and Menodus on the other. Menodus in time, by the loss of its incisors, gave origin to Symborodon. This line left no representatives later than Miocene time. If Epihippus enters this family, it may be the parent of Mesohippus of the next higher horizon, the White River Miocene (Oligocene).

There are numerous species of the genera Menodus and Symborodon, and they are among the most remarkable of Mammalia. They are readily distinguished, among other characters, by the form of the horns. In one group of species they are round except at the tips, and are greatly elongated; in another they are sub-round or slightly compressed; in a third type they are short and trihedral; in a fourth type they are much compressed and expanded transversely; and in a fifth they are of insignificant size. Four of these types exist in both genera. They may be compared as follows:

	Group 1.	Group 2.
Menodus	*M. dolichoceras* S. and O.	*M. coloradoensis* Leidy. *M. giganteus* Leidy. *M. tichoceras* S. and O. *M. angustigenis* Cope.
Symborodon	*S. acer* Cope.	*S. altirostris* Cope. *S. bucco* Cope.

	Group 3.	Group 4.	Group 5.
Menodus	*M. ingens* Marsh.	*M. platyceras* S. and O.	
Symborodon	*S. trigonoceras* Cope.		*S. heloceras* Cope.

Fig. 28. *Symborodon acer* Cope, skull without maxillary and zygomatic bones, one-fifth natural size; left side; from White River beds of Colorado. Original. From Ann. Report U. S. Geol. Survey Terrs., 1873.

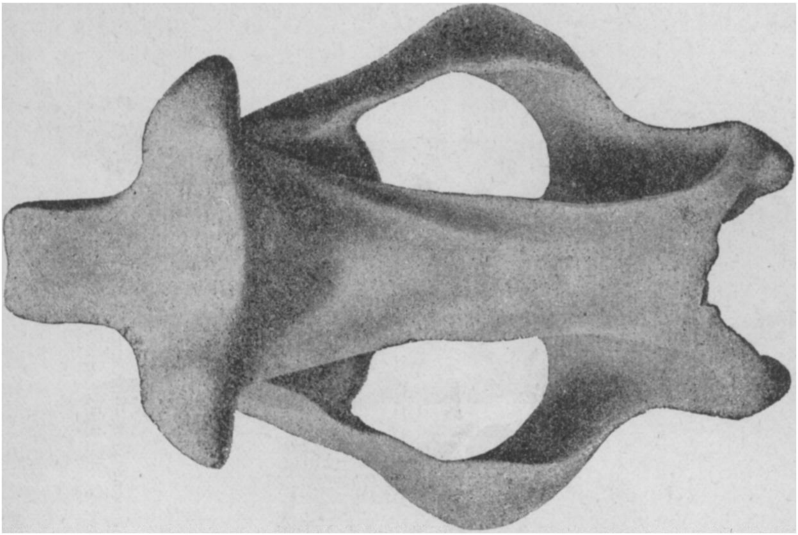


FIG. 29. *Symborodon trigonoceras* Cope, skull from above, one-tenth natural size; from White River bed of Colorado. Original; from "Report U. S. Geol. Survey Terrs." (unpublished).

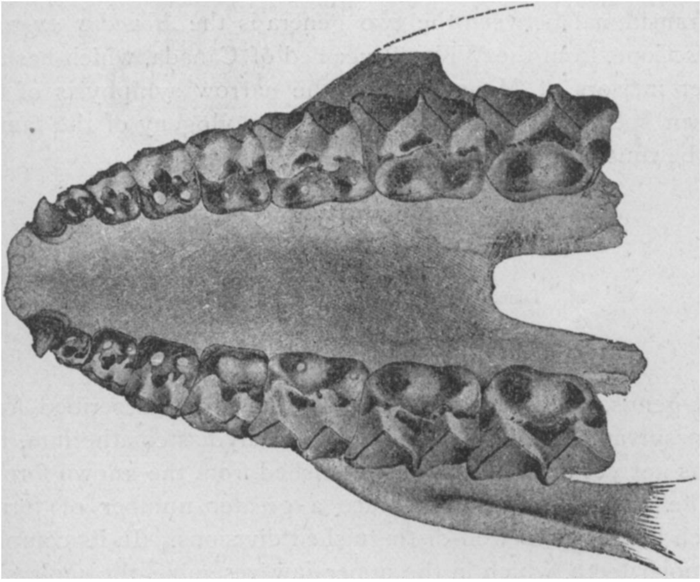


FIG. 30. *Symborodon trigonoceras* Cope, palate and teeth, one-fifth natural size; from White River bed of Colorado. From a different specimen from that represented in Fig. 29. Original; from "Report U. S. Geol. Survey Terrs." (unpublished).

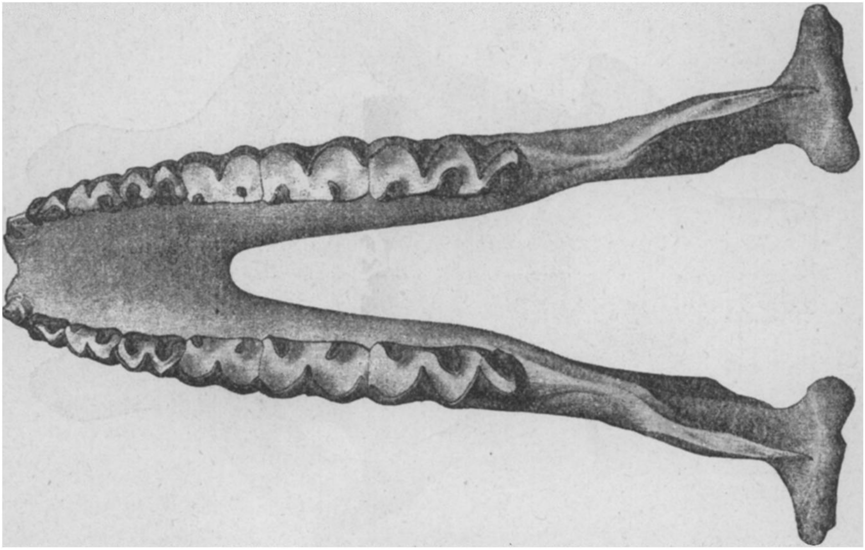


FIG. 31. *Symborodon trigonoceras* Cope, lower jaw from above; from White River beds of Colorado; one-fifth natural size. Original; from "Report U. S. Geol. Survey Terrs." (unpublished).

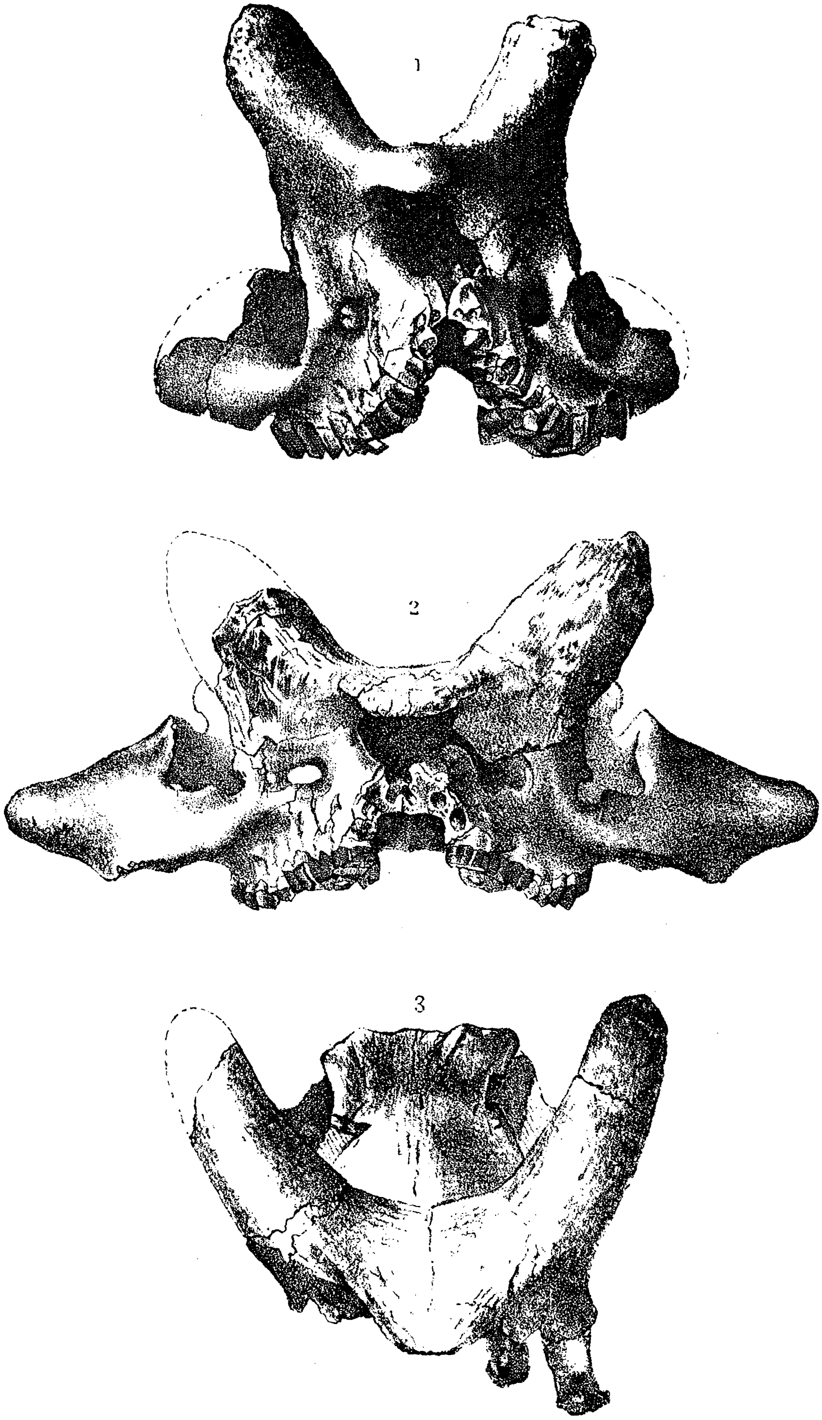
Transitional between the two genera is the *Menodus angustigenis* Cope, from the White River bed of Canada, which has the lower incisors of Menodus, with the narrow symphysis of the known species of Symborodon. The phylogeny of the family can be thus represented:

Symborodon.
/
Menodus.
/
Diacodon. Diplacodon.
\ /
Ectocium.

A genus, probably of this family, has been described from Transsylvania, under the name of Brachydiastematherium, but it has not yet been clearly distinguished from the known forms.

The PALÆOTHERIIDÆ embrace a greater number of forms, which fall into two well-distinguished divisions. In its complex premolar teeth, which in the upper jaw resemble the molars in composition, it shows an advance over the Chalicotheroid and other families of the Lower Eocene. In fact, it has not been found in the Lower Eocene, but commences in the Upper Eocene

PLATE XXXIV.



Front views of skulls of species of Symborodon, one-sixth natural size. Fig. 1, *S. altirostris;* Fig. 2, *bucco;* Fig. 3, *S. acer.* From Ann. Report U. S. Geol. Surv. Terrs., 1873.

in the genera Palæotherium and Paloplotherium. Thence it extends to the very summit of the Miocene, and may even occur in the European Pliocene (Protohippus). Its members exhibit considerable range of variation in the details of the teeth and feet, but no striking break of family importance occurs. The most noteworthy interruption is that which is found between the Palæotherinæ and Hippotheriinæ, where there is a change in the form of the proximal extremity of the humerus from a tapiroid to a horse-like form, and a modification of similar significance in the molar teeth, by the addition of a deposit of cementum.

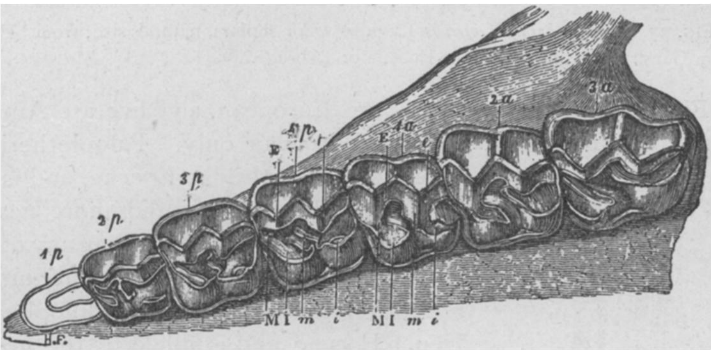


FIG. 32. *Palæotherium crassum* Cuv., superior molars from below, three-quarters natural size; from Gaudry. From the Upper Eocene of Paris.

The characters of the genera are as follows:

I. *Palæotheriinæ.* Bicipital groove of humerus simple; teeth without cementum.

a. One or more internal tubercles of superior molars distinct.

External V's of superior molars not well distinguished externally; .... *Anchilophus.*

External V's separated by a vertical rib; intermediate tubercles not connecting fore and aft; .... *Paloplotherium.*

External V's separated; intermediate tubercles extended fore and aft; .... *Anchippus.*

aa. Internal tubercles of superior true molars continuous with the transverse ridges.

Inferior molars with two V's only; lateral toes large; .... *Palæotherium.*

Inferior molars with distinct internal tubercles; incisors not cupped; .... *Mesohippus.*

Inferior molars with cusps at the inner extremities of the V's; incisors cupped; .... *Anchitherium.*

II. *Hippotheriinæ.* Bicipital groove of humerus double; molars with cement in the valleys. (Intermediate tubercles connected fore and aft; incisors cupped.)

a. One or more internal tubercles of superior molars distinct.
Inner lobes of inferior molars enlarged;.................................*Hippotherium.*
aa. Internal tubercles of molars not distinct.
Inner lobes of inferior molars enlarged;.................................*Protohippus.*

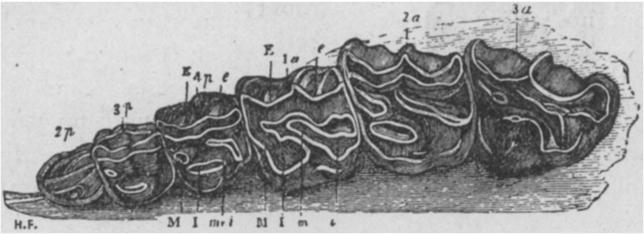


FIG. 33. *Paloplotherium minus* Cuv., superior molars, natural size, from below; from Gaudry. From the Upper Eocene of Lebruge.

Five genera of this family are European, and five are American. The Eocene genera are European only. Paloplotherium is found in the Middle Eocene, and is, as might have been anticipated, more nearly allied to the Chalicotheriidæ than any other genus of this family. Chalicotherium is not far removed from it. Anchilophus is Upper Eocene, and is allied to the genus just named, and also to Pachynolophus among the Chalicotheriidæ. These early genera constitute, by their similarity, the bond of connection between the three families, which, in their later and specialized forms, are very different from each other. Palæotherium is chiefly found in the Upper Eocene, and Mesohippus is only known from the White River or Oligocene, an age between Eocene and Miocene. Anchitherium commences in the Middle Miocene, and has Anchippus for a contemporary. In North America it remained, as late as the Ticholeptus epoch, in the *A. ultimum* Cope. Hippotherium existed only in the latter part of the Miocene epoch, consistently with the greatly specialized structure of its limbs and teeth. The nearly allied Protohippus lived with it, and in Europe a species with the same type of molar teeth is found in the Pliocene epoch (Forsyth-Major). These forms were

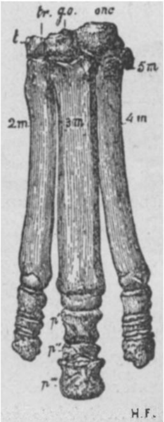
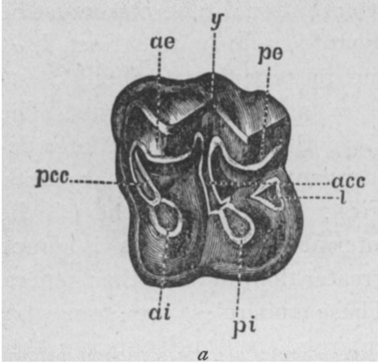


FIG. 34. *Palæotherium medium* Cuv., anterior foot, one-third natural size; from Gaudry. From the Upper Eocene of Paris.

contemporary with the Equidæ, which outlived them. They have many points of resemblance to that family, but, nevertheless, remain at a considerable interval from them in the structure of the feet.



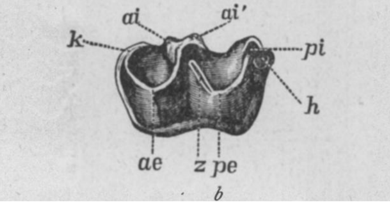


FIG. 35. *Anchitherium aurelianense; a*, superior, and *b*, inferior, molars, natural size; from the Miocene of France; from Gaudry, "Enchainements." Letters, *ae*, anterior external; *pe*, posterior external; *ai*, anterior internal; *pi*, posterior internal, cusps; *pcc*, anterior intermediate; *acc*, median intermediate; *l*, posterior intermediate; *acc*, posterior intermediate, cusps; *k, h*, and *z*, oblique crests.

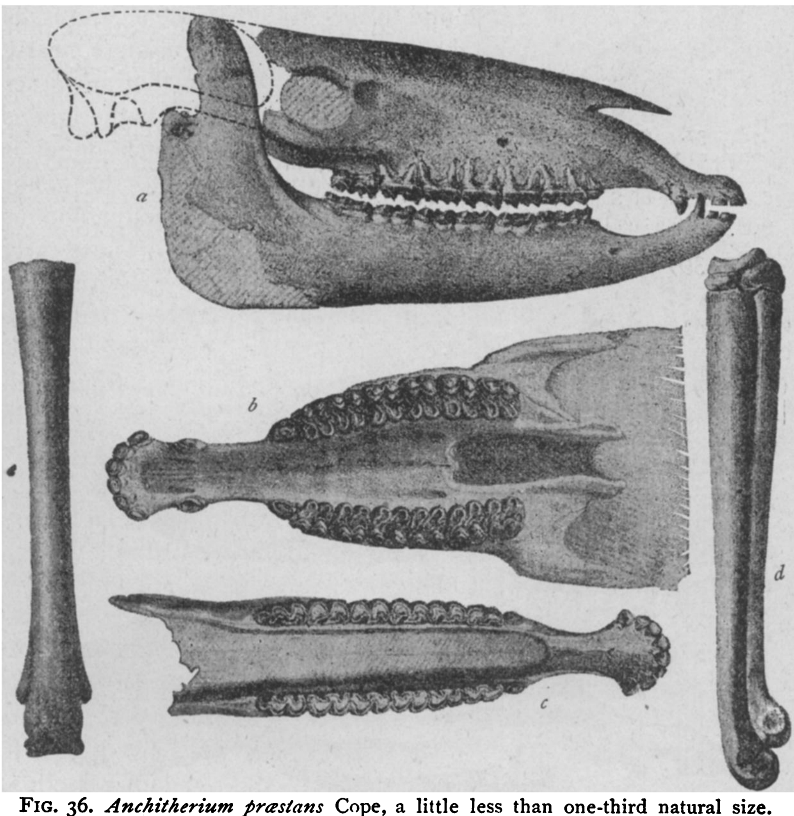


FIG. 36. *Anchitherium præstans* Cope, a little less than one-third natural size. Original; from the John Day (Middle) Miocene of Oregon. Fig. *a*, part of skull, right side; *b*, ditto from below; *c*, lower jaw from above; *d*, metapodial and part of tarsal bones from the inner side; *e*, the metapodials from front.

The phylogeny of the genera of this family is clearly, then, as follows: The genera with distinct internal tubercles must be regarded as primitive (Sect. I, *a*), and those with completed crests (I, *aa*) are derivative forms. The Hippotheriinæ are still later descendants on various accounts. First, the development of the intermediate tubercles is much greater than in any other genera. These tubercles are somewhat enlarged in Anchitherium (see Fig. 35, the anterior one), and they extend much further antero-posteriorly in Anchippus. In the Hippotheriinæ they reach and join each other at the middle of the crown (Fig. 40). In this transition the relations of the internal tubercles are various; for in Hippotherium, one of them (the anterior), remains distinct, while in Protohippus (Fig. 39) both are confluent with the intermediates. It may be

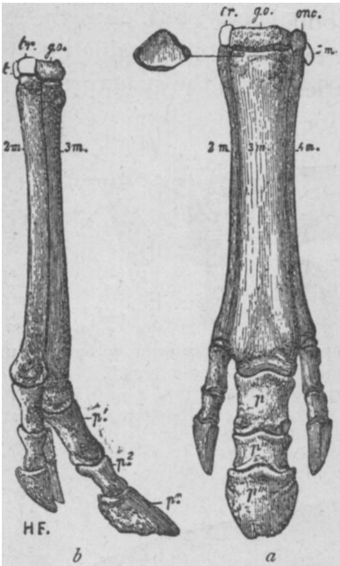


FIG. 37. *Anchitherium aurelianense*, anterior foot, less first carpal row, one-fifth natural size; from Gaudry. From the Miocene of Sansan, France. Fig. *a*, from front; *b*, from right side.

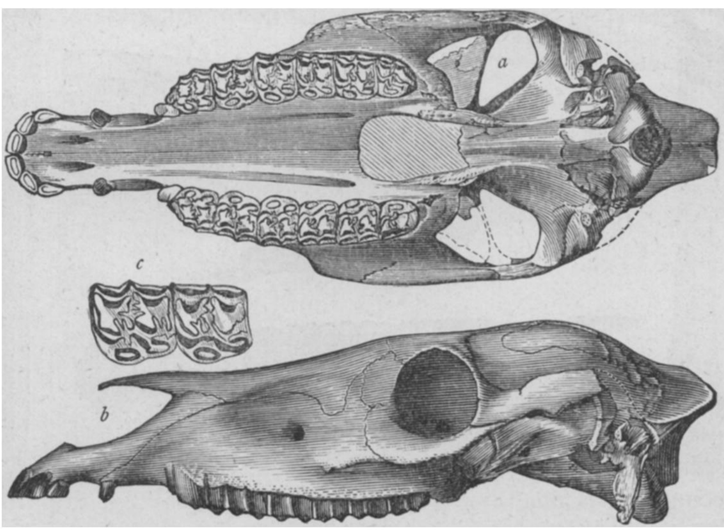
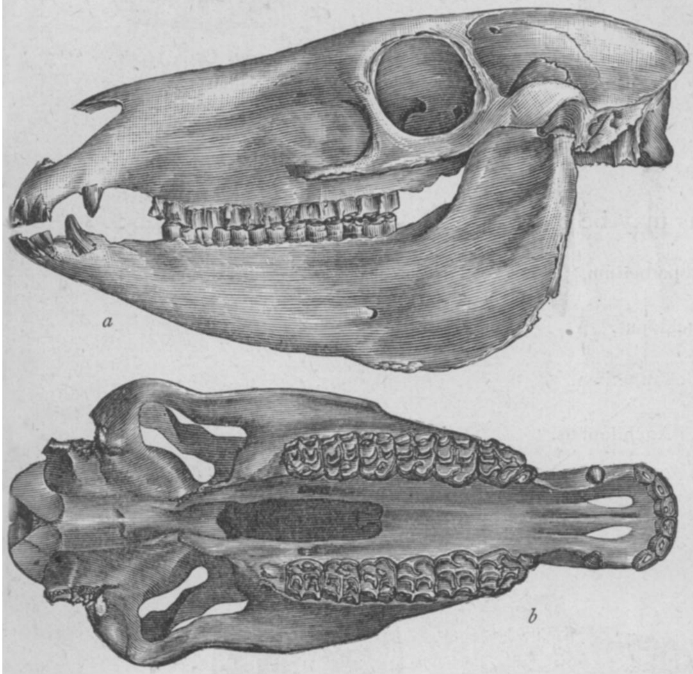


FIG. 38. *Hippotherium speciosum* Leidy, skull, from the Loup Fork bed of Nebraska, one-third natural size. Original. Fig. *a*, from below; *b*, left side; *c*, two superior molar teeth from below.

inferred from this that Hippotherium is a descendant of some genus of Sect. I, *a*, while Protohippus came from a genus of Sect. I, *aa*. The second point of modification to be observed in the Hippotheriinæ is the enlargement of the expansions of the internal extremities of the adjacent horns of the crescents of the inferior molars, which is



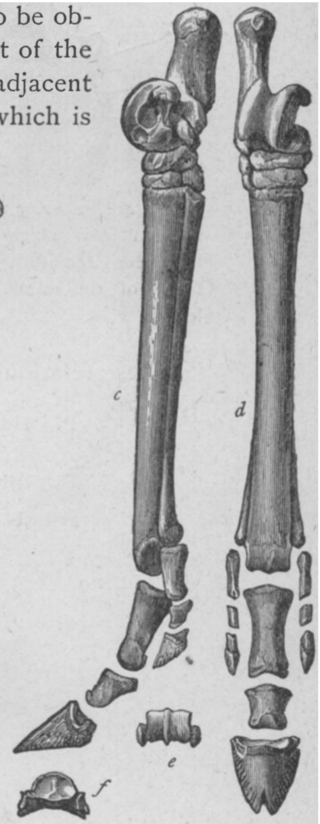


FIG. 39. *Protohippus sejunctus* Cope, one-third natural size. Original; from the Loup Fork Miocene of Colorado. Fig. *a*, skull, left side; *b*, ditto from below; *c*, posterior foot, left side; *d*, ditto, front; *e*, distal end of metapodials; *f*, proximal end of ungual phalange or hoof.

most obvious on wearing, and which are foreshadowed in Anchitherium (Fig. 35, *b*, *ai*, *ai'*). The third evidence of progress is seen in the deposit of cement, which fills the valleys of the teeth. Fourth, the two bicipital grooves of the humerus, which are identical with those seen in the Equidæ. Fifth, the cupping of the crowns of the incisors. This only commences with the genus Anchitherium, the otherwise nearly allied Mesohippus agreeing with Palæotherium and the genera of Sect. I, *a*, in the absence of the cup, as has been shown by Scott.

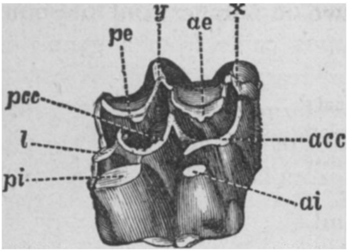


FIG. 40. Superior molar of Hippotherium from which the cementum has been removed, displaying the forms of the crests. From Kowalevsky.

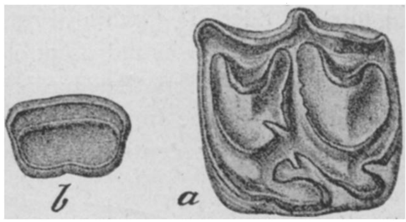


FIG. 41. *Hippidium spectans* Cope, teeth. Original; from Pliocene formation of Oregon. Fig. *a*, superior molar from below; *b*, incisor surface of crown, showing cup. Natural size.

These relations may be expressed as follows, in tabular form:

Hippotherium. Protohippus.
| |
Anchippus. Anchitherium.
| |
Paloplotherium. Mesohippus.
\ /
Anchilophus. Palæotherium.
\ * /
Type with internal cusps and
with fewer premolars like true molars.

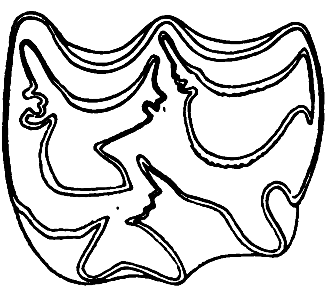


FIG. 42. *Equus crenidens* Cope, superior molar, pattern of enamel-ridges of crown. Original; from Pliocene epoch of Texas. Natural size.

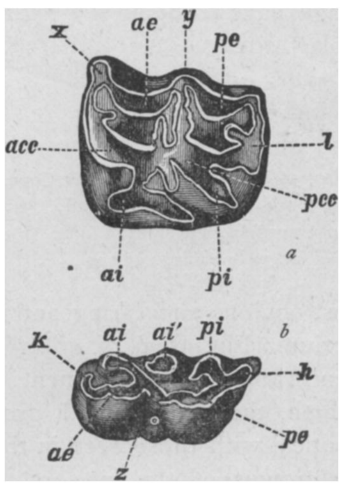


FIG. 43. *Equus caballus* L. *a*, superior, *b*, inferior, true molars. From Gaudry. Five-sixths natural size. Lettering as in Fig. 35.

The genera of EQUIDÆ are but two in number, and they are defined as follows:

Internal lobes of superior molars sub-equal; ....*Hippidium.*
Anterior internal lobes of superior molars much larger than the posterior;...*Equus.*

The genus Hippidium is extinct, and its species have been thus far found only in North and South America, in beds of Pliocene and upper Miocene age. Equus made its appearance during the former period, and is represented by several existing species.

The Equidæ adds another evidence of greater specialization than the Palæotheriidæ in the structure of its feet,—*i.e.*, the distal metapodial keels are completed forwards, as in most ruminants. The mechanical cause of this extension remained, until recently, a puzzle to me. I have endeavored to show that the development of the tongue at the extremity of the metapodials of the Diplarthra was due to the impacts of the terminal phalanges often repeated, on hard ground, together with the compression of the surface on each side the keel by the flexor tendons with their sesamoid bones. But this did not account for the presence of the keel on the anterior face of the extremity. The instantaneous photographs of animals in motion by Muybridge have rendered the explanation easy. He shows that in Diplarthrous ungulates the phalanges are flexed at right angles *anteriorly* on the metapodials, at the last moment of rest on the ground before raising the foot for a new step. This movement is so quickly performed as not to be visible to the ordinary observer. This fact accounts for the late appearance in geological time of its effect on the end of the metapodial bone. I must add here that the acuteness and narrowness of the keel is partly due to the movement of torsion conveyed throughout all the bones of the feet at the moment of arrest by the ground, as referred to in the opening pages of this paper.

I must here describe another effect of torsion of the limbs at the moment of impact of the ungues with the ground, which I omitted from the proper place at the beginning of this paper. The proximal extremities of the metapodial bones are in most mammals extended inwards from the inner towards the outer side of the foot, so as to abut on the carpal or tarsal corresponding to the digit next external to them. This is due to pressure through the carpals and tarsals of the second row or the heads of the metapodials, which is by the torsion turned from within outwards. The pressure thus applied has gradually pressed the heads of the metapodials outwards in the manner described. This effect began earlier than diplarthrism,[1] as it is seen in the Condylarthra.

In the preceding discussion of the phylogeny of the Perissodactyla the descent of genera within families has been described, and also the descent of families in their entireties has been discussed. The attempt to carry the line of generic succession across the boundaries of families has not been generally made. The lack of knowledge of such intermediate genera is the cause of this omission. Were such genera known, the definitions of the families would be less precise than they are. This complete phylogeny has been attempted, however, in the case of the genus Equus by various authors. The first suggestion was made by Cuvier, and the first arrangement of genera in the phylogenetic line of the horses was by Kowalevsky. His series commenced with Anchitherium, and had the other members Hippotherium and Equus. To this series Huxley added Palæotherium. Later, Marsh added two definite terms to the series, Hyracotherium and Hippidium, giving to both, however, new names (Eohippus and Pliohippus), and proposed two other steps (Orohippus and Miohippus), which were not sufficiently characterized to be since recognizable. The present writer determined the identity of the above forms, and added the still more primitive genus Systemodon. He also discovered and defined the Condylarthra, some of which, (Phenacodontidæ), he announced as the ancestor of all Perissodactyla, horses included.[2] Dr. Wortman followed, pointing out the double descent of the genus Equus from the two lines of Palæotheriidæ, and indicating the relations of species

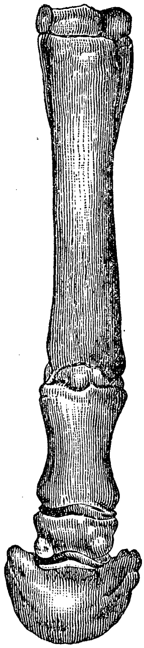


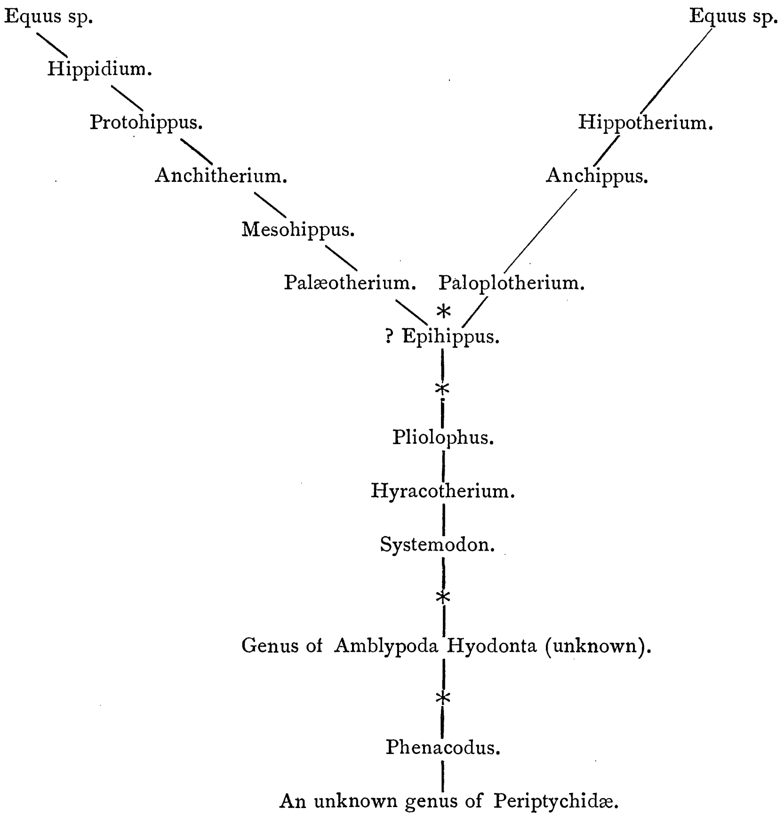
FIG. 44. *Equus caballus* L., manus, much reduced; from Gaudry, "Enchainements."

[1] Cuvier and Kowelevsky have shown that in the genera Sus and Dicotyles the head of the second metapodial is expanded inwards as well as outwards.

[2] Proceeds. Amer. Philosoph. Soc., 1881, p. 178.

of Equus to those of Hippotheriinæ.[1] Subsequently Scott pointed out the relation which the genus Mesohippus (Marsh) bears to the series. Schlosser followed,[2] throwing the Chalicotheriid and Menodontid genera out of the line into which they had been brought by Cope. In the present work the only change the author has made in his views is to return to his inclusion of the Menodontidæ in the line.[3]

As a result the following genealogy of the species of horse may be regarded as resting on the best evidence now available, as regards genera. It will be long before the line of species which has propagated itself to the present day, and appears in the *Equus caballus*, will be discovered.



[1] Revue Scientifique, 1883, p. 705. [2] Morphologisches Jahrbuch, xii., 1886, p. 31.
[3] Amer. Philos. Soc. Proceedings, 1881, p. 380; American Naturalist, 1886, p. 720.

It is certain, if the observation recorded by Mr. G. K. Gilbert is correct, that man was contemporary with species of Equus on the North American continent. I have identified[1] the remains of *Equus occidentalis* Leidy and *Equus excelsus* Leidy from the Upper Pliocene bed of Oregon, where they were mingled with obsidian arrow-heads and scrapers in a sandy bed easily disturbed by the wind. The contemporaneity of these remains being, under such circumstances, uncertain, it remained to discover them in a more solid deposit to confirm the suspicions raised by their association as first observed. Such a discovery is recorded by Dr. Gilbert as having been made in Nevada by a member of the United States Geological Survey. The *Equus occidentalis* thus shown to have been a contemporary of man, is not very close in characters to the true horse, but was proportioned more as in the ass. The head was as large as that of the horse, but the legs were more slender and a little shorter. It ranged from Oregon to Southwestern Texas, but its remains have not yet been found in the Valley of Mexico.

HORNLESS RUMINANTS.

BY R. C. AULD, F.Z.S.

(Continued from page 902.)

England, Wales, and Ireland.

IN treating of British cattle it is of interest to trace their origin. It may therefore be advantageous to quote the views of Prof. Boyd-Dawkins, especially as he has given the subject particular attention, and as I have had some correspondence with him in regard to polled cattle.

"The two principal stocks from which all the breeds are descended are undoubtedly (1) the Urus, an animal wild in the forests of Europe later than the days of Charles the Great, and which, so far as I know, was extinct in the British Isles before the historic period; and (2) the *Bos longifrons*, or 'small Celtic Short-horn,' an animal which never was aboriginally wild in Europe. Both were probably domesticated in Asia, and both make their appearance together in the Neolithic Age, in the

[1] Bulletin U. S. Geol. Survey, 1878, p. 389.