Article VI. — SPECIES OF HYRACOTHERIUM AND ALLIED PERISSODACTYLS FROM THE WAH-SATCH AND WIND RIVER BEDS OF NORTH AMERICA.

By J. L. WORTMAN.

PLATE IL.

The determination of the species of the Perissodactyla from the Lower Eocene horizons of this country has hitherto been a matter of considerable difficulty, and it has been only after a most careful study of nearly all the known material, that I have been able to come to any definite conclusions regarding their classification and arrangement. At the outset it is necessary to clearly distinguish the genera before undertaking to discuss the species.

In the Wahsatch deposits of this country there are only three genera which clearly belong to the Perissodactyla, although several others have been described. The three well-marked groups of species thus capable of being distinguished and defined are Heptodon, Systemodon and Hyracotherium, all of which are found associated in the same deposits. Three others have been proposed, but it is highly probable that they are either synonyms of one of the three above mentioned, or of doubtful generic value.

Of these latter invalid genera I will consider first the one proposed by Prof. Marsh' under the name Eohippus, to which he refers two species, E. validus and E. pernix, the former from the Wahsatch of New Mexico, and the latter from the Wahsatch of the Bear River Beds of western Wyoming. Zittel² considers Echippus and Ectocium, a genus proposed by Cope from the Wahsatch of the Big Horn Basin, as synonymous, but upon what

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From Prof. Marsh's description and ground he does not state. measurements of the two species of this genus it would appear, at least until some other differences are shown to exist, that Echippus validus is the same as Hyracotherium vasacciense of Cope from the same locality. *Eohippus pernix*, according to the measurements and description, corresponds exactly with Hyracotherium index of Cope, also from the same locality in which Prof. Marsh's specimen was obtained.

Prof. Marsh has, however, added some important knowledge to the characters of these earliest known horses, more especially as regards the structure of the feet. He has shown,¹ for example, that in E. validus the hind foot possessed a vestige of the fifth digit, a structure which had entirely disappeared from the horses of the Wind River Beds. He was the first, moreover, to point out the equine characters of these forms. The question now arises, what is the foot structure of the type of Hyracotherium? If it is the same as that described by Marsh in *Eohippus validus*, then Eohippus is a synonym of Hyracotherium, but if it is the same as that described by Cope in Hyracotherium venticolum, viz., the absence of this vestigial fifth digit, then the genus Echippus is a good one and must be retained. The only characters upon which we are enabled to form a judgment is the structure of the superior premolars. These in Owen's type of Hyracotherium² are simple, and correspond closely with the Wahsatch stage of evolution in this country. While in the Wind River horizon, as I will attempt to show presently, there is a decided advance in the structure of one of these teeth, at least, which we know is associated with the disappearance of the vestigial fifth digit from the hind foot, as exemplified in the skeleton of Hyracotherium venticolum. From this evidence it seems to me that one is in a measure justified in considering Echippus and Hyracotherium as referring to one and the same group of species. There is, however, a constant and important difference between the European and American Hyracotheres seen in the structure of the second superior premolar. In all the American forms which I have seen this tooth has two

¹ Amer. Jour. Sci., Vol. XII, Nov., 1876, p. 401. ² Trans. London Geolog. Soc., 2d Series, Vol. VI, p. 203, pl. xxiv.

external cusps, whereas in the European species it is always single, and is therefore more primitive.

I leave for the present the discussion of the propriety of removing those Wind River forms, which exhibit this advanced structure of the premolars and the loss of the vestigial fifth digit, from the genus Hyracotherium or Echippus, and giving to them an independent rank of equal generic value.

The next genus to be considered is *Ectocium*, which was originally proposed by Prof. Cope.¹ A careful comparison by Prof. Osborn of the type specimen with some of the smaller species of Phenacodus reveals the fact that it undoubtedly pertains to this, or some nearly related genus, and is not a member of the Perissodactyla at all.

The third genus to be considered in this connection is the socalled *Pliolophus*, which is not uncommon in the Wahsatch Beds of the Big Horn Basin. The only character by which it is known to differ from the cotemporary Hyracotheres is the presence of a fourth cusp upon the inner posterior part of the last lower premolar, whereby it is said that this tooth is molariform. According to Earle," who has recently examined Owen's type, P. vulpiceps, in the British Museum, the last lower premolar is not entirely molari-This is really the condition of the majority of the form. specimens in the American Museum collection which have been referred to this genus, although it is proper to state here that one can find almost every intermediate stage between the complete absence and the presence of a well-defined cusp in this situation. On this account I am inclined to regard this cusp as at most but a subgeneric variation.

Turning now to the three well-established genera from this formation, I will consider first the characters by which they are distinguished from each other. These characters are summarized in the following table.

¹ Proc. Amer. Phil. Soc., 1881, p. 182. ² American Naturalist, Feb., 1896, p. 132.

| Sub. gen. Pliolophus (?) | (1) Same as in Hyra- cotherium. | (2) Same as in Hyra- cotherium. | (3) Same as in Hyra- cotherium. | (4) Same as in Hyra- cotherium. In one spe- cies diastema absent. | (5) Same as in <i>Hyra-</i> cotherium, except last inferior premolar with two posterior cusps. | (6) Digits, ?-3. |
|-----------------------------|--|--|---|--|---|------------------|
| Hyracotherium. | (I) Ist superior premolar sep- arated by diastema from both canine and 2d premolar. | (2) Internal cusps of superior premolars composed of large lun- ate cusp, with tendency to divide into two cusps. Outline of crown more or less quadrate. Inter- mediate cusps present. | (3) Superior molars with inter- mediates not fused with internal cusps into cross crests, but dis- tinct and well separated. Pos- tero-external cusps not flattened externally nor pushed inwards. | (4) 1st inferior premolar sep- arated by diastemata from both canine and 2d premolar. | (5) Inferior molars without or with slightly developed cross crests, connected by oblique ridge, as in Systemodon. Heel large. Last inferior premolar with single mosterior premolar with single | (6) Digits, ?-4. |
| Heptodon. | (I) Ist superior premolar always in contact with 2d pre- molar and separated by dias- tema from canine. | (2) Same as Systemodon. | (3) Superior molars with intermediates completely fused into cross crests. Posterior external cusps flattened ex- ternally and much pushed inwards. Cross crests high and cutting. | (4) Ist inferior premolar in contact with 2d premolar and separated by diastema from canine. | (5) Inferior molars with perfectcross crests not notched in centre, nor connected by fore and aft oblique ridge. Heel of last molar reduced. | (6) Digits, 4-3. |
| Systemodon. | (1) 1st superior premolar, either separated by diastema from 2d pre- molar or teeth in continuous series. | (2) Internal cusps of superior pre- molars composed largely of single oblique crest, directed forwards and inwards. Outline of crown triangular. No intermediate cusps. | (3) Superior molars with inter- mediates not distinct, but confluent with internal cusps, forming distinct crests. Posterior externally and little pushed inwards; cross crests low and obtuse. | (4) Ist inferior premolar in con- tact with canine and separated by diastema from 2d premolar, or $(?)$ in contact with 2d premolar and sepa- rated from canine by diastema. | (5) Inferior molars with imperfect cross crests notched in centre, con- nected fore and aft with an oblique ridge. Heel of last molar large. | (6) Digits, ?-4. |

TABLE I.-GENERA OF WAHSATCH PERISSODACTVLA.

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Heptodon Cope.

This genus, which is first met with in the Wahsatch and continues in the Wind River Beds, marks the beginning of an important phylum, whose greatest development occurred in the later Bridger and Uinta epochs in America. It is a near relative of *Lophiodon*¹ of the Eocene of Europe, and indeed Cope, who originally proposed the genus, spoke of it as a *Lophiodon* with a full complement of premolars in the upper jaw, whereas *Lophiodon* proper has the first premolar missing.

It differs from its undoubted successor in the Bridger formation, *Helaletes*, in having all the premolars simpler than the molars, while this latter genus has two of the premolars submolariform.

The distinctions between it and Systemodon, its Wahsatch cotemporary, while not marked by any very pronounced characters, is still sufficiently clear to fully warrant the generic separation of the two groups. The more important of these characters are as follows : In Systemodon the superior premolars and canine either form a continuous series or the first premolar is separated from the second by a diastema, being in contact with the canine. In Heptodon the first premolar is always in contact with the second, and there is a considerable diastema between it and the canine. In the superior molars Systemodon has rather low obtuse cross crests, while in Heptodon these cross crests are much higher, sharper and generally better defined. The postero-external cusps (metacones) of the molars of Heptodon are considerably flattened externally and pushed inwards, whereas in Systemodon they are pushed but little inwards and are convex externally. In Heptodon again the first inferior premolar is in contact with the second. and is separated by a diastema from the canine, whereas in Systemodon the first inferior premolar is in contact with the canine and separated by a diastema from the second. It should be stated, however, that the lower jaw of two of the species of Systemodon is not known with certainty as regards this character, but from some fragmentary material of Systemodon semihians it seems probable that the first lower premolar is placed as in the species of Heptodon. I have, therefore, used this character only provisionally. Some further differences are to be seen in the

¹See Bull, Am. Mus. Nat. Hist., Vol. VII, 1895, p. 361.

lower teeth which serve to distinguish the two genera from each other quite clearly. The cross crests of the lower molars of Systemodon are less perfectly developed, and the anterior and posterior crests are always connected longitudinally by an oblique ridge; in *Heptodon* the cross crests are better developed, just as in the superior molars, and the oblique fore and aft ridge is entirely wanting. In Heptodon, moreover, the heel of the last molar is much reduced and pointed, while in Systemodon it is large, broad and prominent. This reduction of the heel, I take it, is in some way associated with the pushing in of the metacone and shortening of the posterior cross crest of the last superior molar, which is always most pronounced in this tooth, indicating its remote affinity to the Rhinocerotoidea.

As compared with Hyracotherium, the position of the first superior premolar in both jaws, the internal cusps of the superior premolars, as well as the structure of the molars, distinguish Heptodon at once from this genus. These characters are fully set forth in the foregoing table and need no further mention.

The species of *Heptodon* are not numerous, two having been described by Cope from the Wahsatch and two from the Wind River Beds; one of these, *H. singularis*, is as yet very imperfectly known, and it may prove to belong to another genus. It is from the Wahsatch of New Mexico. The other Wahsatch species, H. posticus, is represented by two lower jaws from the Big Horn Beds (Nos. 4687 and 4688), while the two Wind River species, H. calciculus and H. ventorum, are better known.

The definitions of these species are as follows :

| H. posticus | H. calciculus | H. ventorum | H. singularis |
|---------------------|--------------------|--------------------|---------------------------------------|
| Cope. ¹ | Cope. ² | Cope. ⁸ | Cope. ⁴ |
| (I) Upper teeth | (1) 2d upper | (1) 2d upper | (1) 2d upper |
| unknown. | | premolar with two | premolar unknown. |
| () | gle external cusp. | | |
| (2) 4th lower | (2) 4th lower | (2) 4th lower | (2) Lower teeth |
| premolar with sin- | | | unknown. |
| gle posterior cusp. | in H. posticus. | posterior cusps. | · · · · · · · · · · · · · · · · · · · |
| (3) Length of 3 | (3) Length of | (3) Length of 3 | (3) Unknown. |
| lower molars and 3 | 3 lower molars and | lower molars and | |
| lower premolars, | 3 lower premolars? | 3 lower premolars? | |
| 62 and 66 mm. | | | |
| (4) Upper mo- | | (4) Length of | |
| lars unknown. | | upper molars and | |
| | | 3d and 4th premo- | |
| | lars, 48 mm. | lars, 47 mm. | lars, 32 mm. |

¹ Proc. American Philos. Soc., 1881, p. 187. Am. Nat., 1882, p. 1029.
² Am. Nat., 1880, p. 747.
³ Am. Nat., 1880, p. 747.
⁴ Wheeler Surv., IV, ii, pl. lxvi.

1896.] Wortman, Species of Hyracotherium.

As already remarked, the larger Wahsatch species, *H. posticus*, is known from two lower jaws, which differ somewhat from each other in size. The smaller of these (No. 4688) Cope referred to *H. ventorum*, but it differs from this species not only in the simpler fourth premolar of the lower jaw, but in the less elevated and more obtuse crests of the molars. From *H. calciculus* it differs, so far as we now know, only in size, but, considering the wide separation in point of time, there can be little doubt that other important differences will be found when we know more of its skeleton. For a fuller description of the Wind River species I must refer the reader to Prof. Osborn's paper¹ as well as the work of Prof. Cope.²

Systemodon Cope.

The species of this genus have thus far been found only in the Wahsatch. The distinctions between it and *Heptodon* have already been fully considered. Its morphological position, so far as I am able to judge from the fragmentary material by which it is represented, is intermediate between that of *Heptodon* and *Hyracotherium*. With the exception of the position of the

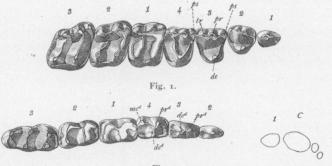


Fig. 2.

Figs. 1 and 2. Systemodon protapirinus. Type specimen, No. 4460, Wahsatch Beds, Big Horn, Wyoming. Natural size.

Fig. 1. Upper teeth, crown view. ABBREVIATIONS: pr.=protocone, de.=deuterocone, tr.=tritocone, ps.=parastyle. Fig. 2. Lower teeth, crown view. ABBREVIATIONS: prd.=protoconid, ded.=deuteroconid, $me^{d}.=$ metaconid.

¹ Bull. Amer. Mus., Vol. IV, Oct., 1892, p. 128, in which the foot structure of *H. calciculus* is described. ² Tertiary Vertebrata, p. 656. first lower premolar, it exhibits all the characters which we would be led to look for in the ancestor of *Heptodon*. This latter character, it is proper to remark, is not known with certainty except in one species, and it may yet prove that one of the other species fulfills all the requirements of the ancestral species.

Systemodon differs from Hyracotherium in the following characters: In Hyracotherium the first premolar in both jaws is separated by a diastema from the canine in front and the second premolar behind; in Systemodon, as we have already seen, it varies with the species. The internal cusps of the superior premolars in Systemodon consist of oblique crests without intermediates, while in Hyracotherium these cusps are large and lunate, with a tendency to divide into two, always associated with intermediates in some of the premolars. In Hyracotherium the outline of the crowns of the third and fourth premolars are more quadrate than in Systemodon, because of the large lunate internal cusp. In the upper molars of Systemodon, the intermediates are fused with the internal cusps, so as to form cross crests, while in Hyracotherium the intermediates are perfectly distinct. The same cresting of the lower molars is seen in Systemodon, but while some species of Hyracotherium show a marked tendency in this direction they are never so fully crested as in Systemodon.

In the foregoing table of the generic characters, mention has been made of the foot structure of the several genera. This is well known in *Heptodon*¹ and *Hyracotherium*, but that of *Systemodon* has hitherto been unknown. I will merely mention here that so far as the hind foot is concerned, *Systemodon* resembles *Heptodon* to a remarkable extent. This likeness is seen in the compressed elongated character of the foot as well as in the great length and slenderness of the phalanges. In *Hyracotherium* the phalanges are short, a character which distinguishes them at a glance. In *Systemodon* there was at least a vestige of a fifth digit, and so far as one is able to judge from the material, I am inclined to the opinion that this digit was complete.

Three species are known with certainty, all of which are from the Wahsatch. They are defined as follows:

¹ Bull. Am. Mus. Nat. Hist., Vol. IV, 1892, p. 128.

S. protapirinum.1 S. primævus. S. semihians sp. nov. Cope. sp. nov. (1) Premolars and ca-(1) Premolars and (1) A diastema between nine in continuous series canines in continuous 1st and 2d superior prein upper jaw. series in upper jaw. molars. (2) Second superior (2) Second superior (2) Second superior prepremolar with strong inpremolar without inter- molar with small internal ternal cusps. nal cusp. cusp.

Systemodon primævus, sp. nov.

This species is indicated in the collection by two fragments of skulls (Nos. 144, 147) supporting the entire superior dentition. There are several other skull fragments in the collection which doubtless pertain to the same species, but the characteristic second premolar is not sufficiently preserved to determine this point with certainty.



Fig. 3. Systemodon primævus. Upper teeth, crown view (type specimen, No. 144). Wahsatch Beds, Big Horn, Wyoming. Natural size. ABBREVIATIONS: pr.= protocone, de.= deuterocone, tr.=tritocone, pl.=paraconule, ps.= parastyle.

The specimen which I select as the type of the species is No. 144; it includes the two superior maxillaries and premaxillaries containing all the teeth. The structure of the superior molars and premolars, as well as the absence of diastema, refer it to *Systemodon* without question.

As compared with *S. protapirinum* it exhibits the same size and otherwise resembles it closely in every way except in the structure of the second superior premolar. In *S. primævus* this tooth has no internal cusp, whereas in *S. protapirinum* there is a strong internal cusp. From *S. semihians* it is readily distinguished by the presence of a considerable diastema between the first and second superior premolars in this latter species.

¹ The type of this species was originally referred to Hyracotherium, and afterwards to Systemodon. I find that the original generic reference was correct, and that this species requires a new name, which I here give to it.

1896.]

The principal measurements are as follows :

| ν. | мм. |
|--|-----|
| Lingh of promotion and motion to the second second | 63 |
| Length of premolars | 32 |

A fairly well-preserved specimen of a hind foot (No. 234) of a species of *Systemodon* is preserved in the collection, which it is proper to describe in this connection.¹ Although it is accompanied with nearly all the teeth of the lower jaw, the characteristic parts of the upper jaw are not preserved, the only means known at present by which the species can be determined with certainty. The lower jaw agrees very closely with that of *Systemodon protapirinum*, and it is highly probable that the specimen belongs to this species.

The general character of the foot is strikingly like that of Heptodon; this is especially seen in its comparative slenderness, the form of the astragalus, the calcaneo-fibular facet, the elongated metapodials, and above all in the extreme length and slenderness of the phalanges. As has already been shown² the astragalus and calcaneum of Heptodon are so very decidedly equine in appearance that it is indeed difficult to distinguish them at first sight in the three genera. There is a character. however, which was originally pointed out by Prof. Osborn,³ viz. : the union or confluence of the ectal and sustentacular facets of the astragalus in all the Perissodactyla with the exception of the horses, which I find holds good in the Perissodactyla of the Wahsatch. Heptodon and Systemodon agree in having these facets confluent, while in the horses these facets are separated from each other.

The relations of the tarsal elements are very similar to those of *Heptodon*, as are also the characters of the bones themselves. One point of especial interest is the number of digits. Besides the usual three, the fourth metapodial exhibits a well-marked facet upon the posterior surface of its proximal end, which undoubtedly served for the articulation of the fifth metapodial. It may be that this metapodial was only vestigial in character, a

¹ Mention of this specimen has already been made in a former paper in the Museum Bulletin. See Art. XI, Vol. V, p. 170.

² Bull. Amer. Mus., Vol. IV, Article XI, 1892, p. 128.

⁸ Mammalia of the Uinta Formation.

fact which would seem to be indicated by its having lost all connection with the cuboid. The exact length of the metapodials cannot be determined on account of their damaged condition, but enough is indicated to state that the foot was relatively long and slender. Several phalanges are preserved, and, as already remarked, their chief peculiarity consists in their great length. No ungual phalanges are known.

Hyracotherium Owen.

The differences between this genus and its two Wahsatch cotemporaries, *Systemodon* and *Heptodon*, have already been considered; it now remains to compare it with its successors in the Wind River and Bridger epochs. I have already called attention to the fact that certain of the Wind River forms show a marked advance in the structure of the third superior premolar, which we know to be associated with the loss of the vestigial fifth digit in the hind foot. This conclusion, it may be stated, is not based upon a single specimen, but upon at least two, in which it can be determined with certainty (Nos. 4832 and 4848). We have then two trenchant morphological characters, modifications which point strongly in the direction of the subsequent changes which the horses underwent in later times.

According to all customs of palæontological nomenclature the Wind River type exhibiting these characters should be separated as a distinct genus, and although it may seem unwise to still further complicate the already overcrowded list of generic names for these early horses, yet I am strongly of the opinion that it is really necessary if we wish to truly express with our nomenclature the major and minor changes to which this steadily advancing phylum was subjected.

Additional characters which distinguish the more advanced Wind River species from the Wahsatch forms are seen in the subcrescentic form of the outer cusps of the superior molars, as well as the lengthening of all the cusps of these teeth, the presence of a rudimentary mesostyle and the appearance for the first time of a small but distinct hypostyle. Upon these characters, therefore, I propose a new genus, which may be known as *Protoro*- *hippus.* The Eocene genera of the American Equidæ may then be defined as follows :

| Hyracotherium. (Eohippus.) (Wahsatch.) | Protorohippus, gen. nov. (Wind River.) | Orohippus. (Pachynolophus) (Bridger.) | <i>Epihippus.</i> (Uinta.) |
|---|---|--|---|
| (1) A vestige of the fifth digit in the hind foot. | | (1) Same. | (1) Same. |
| (2) Outer cusps of superior molars subconic. | | (2) Outer cusps of superior molars subcrescentic. | (2) Same. |
| (3) No trace of mesostyle. | (3) Rudimental mesostyle. | (3) Mesostyle complete. | (3) Same. |
| (4) No trace of hypostyle. | (4) Rudimental hypostyle usually present. | (4) Hypostyle stronger. | (4) Hypostyle well developed. |
| (5) Third supe- rior premolar with three well devel- oped cusps and only a trace of the fourth cusp. | four well-developed cusps. Second | fourth superior premolars molari- form. Second su- | fourth superior premolars molari- form. Second su- perior premolar |

TABLE II.—GENERA OF AMERICAN EOCENE HORSES.

I have here used the names *Orohippus* and *Pachynolophus* as possibly synonymous, as has been done by Zittel and Osborn. I do not know the type of *Pachynolophus*, and it is apparently not at all certain to what species it was originally applied. If Rütimeyer has correctly referred his specimen of an upper jaw to *Pachynolophus sideroliticus*, or if Kowalewsky has properly identified and figured the upper molars and premolars of *Pachynolophus desmaresti*,¹ then it would seem certain that the course of the evolution of the superior premolars has been very different in the European and American species of the corresponding stage of development, and that these two series represent

¹See Zittel's 'Handbuch der Paleontologie' for figures of *P. sideroliticus* and *P. desmaresti*, p. 242, 243.

distinct phyla. If this supposition is true, then the genus *Pachy-nolophus*, as understood by European authors, does not occur in the Eocene deposits of this country, and its corresponding stage of evolution among the American horses is represented by the genus *Orohippus* of Marsh.

| | | WAHSATCH. | | WIND River. | BRIDGER. | UINTA. | |
|---------------|----------------|------------|--------------|----------------|-----------|--------|---|
| | | N. Mex. | Big Horn. | Bear River | | | |
| Hyracotheriu | n cristatum | | .× | | | | |
| " | vasacciense | .× | .× | | | | |
| " | tapirinum | | | | | | |
| " " | craspedotum | | | | × | | |
| " | index | .× | .× | .× | | | |
| H. (Pliolophu | s) cristonense | .× | .× | | | | |
| ** | montanum | | .× | | | | |
| Protorohippus | venticolum | ••••• | | | × | | |
| Orohippus | | | | | | × | |
| Epihippus | •••••• | | | | . | | × |

GEOLOGICAL DISTRIBUTION OF THE HYRACOTHERES.

The discrimination of the species of *Hyracotherium* is indeed a difficult task, owing partly to the very imperfect specimens that were used by Cope as types in the original descriptions of the species, and partly to the wide limits of individual variation that must be admitted in these forms. My own specific determinations are based upon the materials contained in the American Museum collections, together with the types of Cope's species from the Wahsatch of New Mexico, preserved in the National Museum. Unfortunately I have not been able to include Prof. Marsh's material from the New Mexican and Wyoming Wahsatch, but as he has described only two species from this horizon, already alluded to above, I feel reasonably certain that the more important modifications are included in the subjoined table. The characters of the species are as follows:

| H. tapirinum Cope. | H. cristatum, sp. nov. | H. craspedo- tum Cope. | H. vasacciense Cope. | H. index Cope. |
|-----------------------------------|---------------------------------------|---|--------------------------------------|---|
| third and fourth premolars and | third and fourth premolars and | (1) Length of third and fourth premolars and lower molars, 49 mm. | molars and third and fourth lower | third and fourth premolars and |
| | | (2) Third lower premolar with two anterior cusps. | | premolar with two |
| last lower molar | last lower molar large; tooth long | (3) Heel of last lower molar large; tooth rela- tively broad. | last lower molar | (3) Heel of last lower molar large; tooth long and narrow. |
| cusps of last lower molar sep- | cusps of last | molar separated | (4) Same. | (4) Same. |

TABLE III.-SPECIES OF WAHSATCH AND WIND RIVER HYRACOTHERES.

Hyracotherium tapirinum¹ Cope.

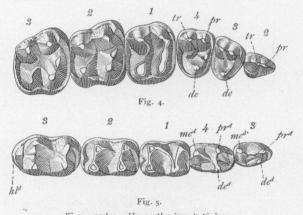
Systemodon tapirinum.

This is one of the largest species of all the Wahsatch Hyracotheres. It was originally described by Cope from the Wahsatch of New Mexico from two fragments of lower jaws. One of these (1064, Nat. Mus. Coll.) contains the last two molars, but is in such a very worn and damaged condition as to be practically valueless for the determination of the characters of the species. A second fragment (1083, Nat. Mus. Coll.), containing the second molar in a good state of preservation however, shows the characters much better, and demonstrates beyond any doubt that it belongs to *Hyracotherium* and not to *Systemodon*, as Cope afterwards concluded, and has subsequently referred it. Additional material, including nearly all the upper and lower teeth with the exception of the upper and lower incisors and canines, is

¹Cat. Eoc. Vert. New Mexico, 1875, p. 20. Amer. Nat., 1881, p. 1018. Tert. Vertebrata, p. 619 (referred to Systemodon).

now contained in the collections of the Museum, which permit of a fuller determination of the species.

These materials are (1) a fragment of lower jaw supporting the last two molars (No. 143*a*); (2) upper and lower molars of both sides, together with lower premolars 3 and 4, and the fourth upper premolar (No. 4657); (3) a palatal portion of a skull containing all the molars, together with the third and fourth premolars (No. 212); and (4) upper and lower molars associated with second superior premolar (No. 139). Since no one specimen gives all the characters of the dentition, the accompanying drawing has been constructed from these several specimens.



Figs. 4 and 5. Hyracotherium tapirinum. Fig. 4. Upper teeth, crown view (composition from Nos. 139 and 212). Wahsatch, Big Horn. X $\frac{4}{3}$. Fig. 5. Lower teeth, crown view (composition from Nos. 143a and 4647). Wahsatch, Big Horn. X $\frac{4}{3}$. ABBREVIATIONS: pr=protocone, de.=deuterocone, tr.=tritocone, prd.=protoconid, ded.=deuteroconid, med.=metaconid, ht^{d} .=hypoconulid.

The *characters of the species* are as follows: Species large; the length of the lower molars and premolar 3 and 4, 49 mm. The heel of the last lower molar is relatively small and conic, and the cross crests are well developed with the exception of that connecting the two posterior cusps of the last molar, which are separated by a deep notch. The second lower premolar has a well-developed second anterior cusp. The antero-internal cusps of the lower molars are not bifid at their extremities. In the upper molars the intermediates are hardly as distinct as in some of the smaller species; the fourth superior premolar has very distinct intermediates, and the second displays two distinct external cusps. The measurements of the teeth are as follows :

L

| | of the 3d and 4th premolars and three lower molars last lower molar |
|----|--|
| | |
| | molars I and 2 |
| ** | 3d and 4th lower premolars |
| •• | upper molars and premolars 2, 3 and 4 |
| | upper molars |
| | upper premolars 2, 3 and 4 |

The species is so far known from the Wahsatch of New Mexico and the Big Horn Basin, Wyoming. The specimens referred to it are Nos. 139, 143*a*, 212, 4598, 4650, 4651, and 4657.

Hyracotherium cristatum, sp. nov.

This large species of Hyracotherium is represented in the collection by five or six specimens from the Wahsatch of the Big Horn Basin. It is about equal in size to H. tapirinum, but differs from it markedly in the structure of the third lower premolar, which lacks the antero-internal cusp. The antero-internal cusp of the fourth premolar is also much less developed, and has a



Fig. 6. Hyracotherium cristatum. Lower teeth, crown view (composition from Nos. 240 and 248B, Type specimens). Wahsatch Beds, Big Horn. X $\frac{4}{3}$.

more posterior position than in *H. tapirinum*. The heel of the last molar is relatively much larger, the cusps are more elevated, and the antero-internal cusps of the lower molars are slightly bifid. The cross crests of the lower molars are well developed, that between the posterior cusps of the last molar being as well developed as the others.

Two superior molars associated with lower molars are contained in the collection, which serve to demonstrate that it belongs to *Hyracotherium* and not to *Systemodon*, as the extreme cresting of 1896.]

the lower molars would seem to indicate. The superior premolars are unknown. The measurements are as follows :

| | | IVI IVI + |
|---|---------------------------------------|-----------|
| | 3d and 4th lower premolars and molars | |
| | last lower molar | 14.5 |
| " | molars 1 and 2 | 20 |
| " | premolars 3 and 4 | 15 |

The *type* of this species consists of two specimens, one (No. 258b) a fragment of a lower jaw bearing the first and second molars, and the third and fourth premolars, and another, a fragment of a lower jaw (No. 240) containing the last molar; both from the Wahsatch of the Big Horn Basin. To it may also be referred Nos. 4653-6, from the same locality.

Hyracotherium craspedotum¹ Cope.

Cope's type of this species consists of a lower jaw (No. 4830), one side containing the three molars and a part of the last premolar, the other side containing premolars 2 and 4 with the first molar, from the Wind River Basin. There is also a skull (No. 4831) in the collection from the same horizon which contains nearly all the upper teeth with the exception of the incisors and canines; notwithstanding that it is somewhat smaller than the type it has been referred to the same species.

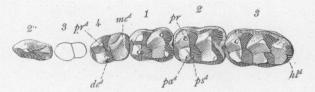


Fig. 7. Hyracotherium craspedotum. Lower teeth, crown view (type specimen, No. 4830). Wind River Beds, Wyoming. X_3^4 .

The characters of this species indicate that it is closely related to, and very probably the direct successor of, *H. tapirinum* of the Wahsatch. Unfortunately the third lower premolar is not preserved, so it is impossible to say whether it agrees with *H. cristatum* or *H. tapirinum* in the structure of this tooth. It is more than probable, however, that it will be found to agree with

¹ Amer. Nat., 1880, p. 747; Tert. Vert., p. 631.

[June, 1896.]

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the latter of these species in this character, since the presence of this antero-internal cusp constitutes an advance in the structure of the premolars, and it would be remarkable indeed if a Wind River species were so backward in this particular as to have this cusp lacking.

It differs considerably from *H. tapirinum* in the size of the heel of the last lower molar, which is large, and inclined to be more or less basin-shaped. It also differs from this species in having a much greater width of the lower molars in proportion to their length. The extreme, among the large species, of the long and narrow lower molars is seen in *H. cristatum*. The cusps of the lower molars of the species under consideration are low and obtuse, and the cross crests are but very little developed—an additional character which distinguishes it sharply from *H. cristatum*. The antero-internal cusps of the lower molars are slightly bifd at their extremities, presenting a parastylid. The superior molars do not present any differences worthy of note from those of *H. tapirinum*.

The measurements are as follows:

| | | IVI IVI . |
|-----------|--|-----------|
| Length of | 3d and 4th premolars and lower molars | .49 |
| | last lower molar | 14 |
| | molars I and 2 | 19.5 |
| | premolars 3 and 4 | |
| " | superior molars and 3d and 4th premolars | 42 |

Hyracotherium vasacciense¹ Cope.

The *type* of this species consists of a single lower molar (No. 4658) from the Wahsatch of New Mexico, which I take to be the

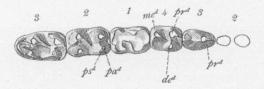


Fig. 8. Hyracotherium vasacciense. Lower teeth, crown view (No. 4659). Wahsatch Beds, Big Horn Valley, Wyoming. X $\frac{4}{3}.$

¹ Proc. Am. Phil. Soc., 1872, p. 474 ; Tert. Vert., p. 634.

It is wholly uncharacteristic, and the reference of any second. additional material to it is, according to the very nature of the case, attended with uncertainty. Cope subsequently obtained other material more characteristic which he referred to this species,¹ and distinguished the species by the depth of the ramus. This character I find is exceedingly variable, and appears to be in a large measure dependent upon the age of the individual. If we are to accept Cope's determinations, then, in my judgment, the species will have to be abandoned, since there are no means discoverable, with the present material at least, by which it can be distinguished from *H. index*. There is in our collection from the Big Horn an almost complete jaw (No. 4659) containing all the molars, together with the third and fourth premolars, which I prefer to take as representing this species. I do this for three reasons, viz.: (1) It agrees quite as well with the uncharacteristic type as does any other specimen which has been referred to it; (2) by so considering it the species is capable of definition, and (3)the proposing of a new specific name will be avoided.

The character of the species thus considered would then be as follows : The ramus is remarkable for its great depth in comparison with the size of the teeth; the third lower premolar is without the antero-internal cusps; the last lower molar is unusually short and broad with a relatively small heel. The measurements are :

| Length of | 3d and 4th premolars and lower molars | мм. 38 |
|-----------|---------------------------------------|-----------|
| ٩, | last lower molar | 10 |
| | molars 1 and 2 | |
| " " | premolars 3 and 4 | 13 |

Beside those already mentioned, two other individuals, Nos. 4660 and 4661, are referred to this species.

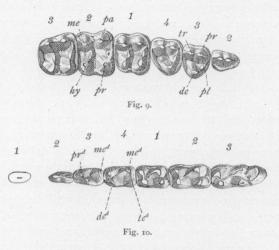
Hyracotherium index² Cope.

Under this heading I arrange all the specimens which Cope has referred to H. index, H. angustidens, H. cuspidatum, all, in fact,

 ¹ Wheeler Surv. Rep., Vol. IV, Part ii, p. 264.
² Bull. Hayden Surv., 1873, p. 459; Wheeler Surv. Rep., IV, Pt. ii, p. 262; Tertiary Vert., p. 650.

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except the type, which he has referred to *H. vasacciense*, as well as all the *Wahsatch* specimens classified under the name of *H. venticolum*. I also place here Cope's specimens identified as *Orotherium vintanum* (Marsh) from the New Mexican Wahsatch. The



Figs. 9 and 10. Hyracotherium index. Fig. 9. Upper teeth, crown view (No. 4602). Wahsatch Beds, Big Horn Valley, Wyoming. Fig. 10. Lower teeth, crown view (No. 4613). Wahsatch Beds, Big Horn. X 4.

type of this latter species was originally described by Marsh from "specimens found on Henry's Fork in the Bridger Basin, and it is very much more probable that it belongs to *Orohippus* than to *Hyracotherium*.

In bringing together all of these so-called species I am sensible of the fact that it associates individuals which differ from each other considerably in the matter of size and the depth of the ramus, but there are such perfect gradations in this respect among the large number of individuals which we now possess, that I find it utterly impossible to make any valid distinctions, and it is perhaps better to err on the side of safety and have too few species than to admit a larger number which cannot be defined.

The species thus constituted exhibits a very great constancy in the structure and proportions of the teeth, from which it is almost exclusively known. The *specific characters* may be summarized as 1896.]

follows: The third lower molar is very long and narrow in proportion to its width; the heel is large, prominent, and has but a single pointed cusp. The cusps of the lower molars are well separated, with very little tendency to form crests, and the third lower premolar has two anterior cusps. There is a very considerable difference in size, together with marked differences in the depth of the mandibular ramus, but, as already remarked, this latter character is in some measure due to the age of the individual.

The species is at once distinguished from H. vasacciense and H. cristatum by the more complex character of the third lower premolar; from H. tapirinum it differs not only in size, but in the much narrower and relatively longer last molar, the relative size of the heel of this tooth, and the degree of separation of the cusps of all the lower molars. From H. craspedotum it can readily be distinguished by the much smaller size, and the general narrowness of the lower teeth in proportion to their width. In H. craspedotum, moreover, the cusps are much more robust and less elevated. The following measurements indicate the range in size of the individual :

| | MM. | мм. | мм. | мм. | ММ. | мм. |
|-----------------------------|-----|------|------|-----|------|-------|
| Length of premolars 3 and 4 | | | | | | TYPE. |
| and lower molars | 36 | 32 | | | 38 | 31 |
| Length of last lower molar | | 10.5 | 12 | 10 | 09.5 | 09 |
| " molars 1 and 2 | | 14 | 17.5 | 15 | 16.5 | 11.5 |
| " premolars 3 and 4 | 12 | 12 | | | 12 | 10 |

All of the foregoing species of *Hyracotherium* are readily distinguished from the European species *H. duvali* and *H. leporinum*, by the greater simplicity of sup. pm. 2, which in these latter species has but a single external cusp. In all the American species this tooth has two external cusps. It may yet be found that there are other important differences between these groups which will necessitate recognizing a separate genus for the American forms, in which event the name *Eohippus*, proposed by Marsh, would have to be adopted.

Subgenus Pliolophus Owen.

As already remarked, this is a genus of very doubtful validity. A number of specimens occur in our collections in which the fourth lower premolar has a more or less distinct fourth cusp. In no instance in which I have observed it, however, can this tooth be said to be fully molariform, almost all degrees of distinctness being met with. With few exceptions these specimens agree in every respect with H. index, and whether they are to be regarded as of generic importance, or are best treated as specific variations, is a question difficult to determine. From the very great similarity between these specimens and those of H. index, as well as the great variability in the size of the cusp in question, one is almost tempted to believe that they are only individual variations of this species. I will consider them here under the subgeneric title *Pliolophus*.

Hyracotherium (Pliolophus) cristonense¹ Cope.

The type of this species consists of an almost entire mandible lacking only the posterior portion (No. 1002, Nat. Mus. Coll.); it

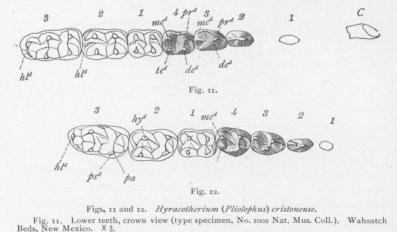


Fig. 12. Lower teeth, crown view (No. 165). Wahsatch Beds, Big Horn. X 4.

¹ Wheeler Surv. Reports, IV, p. 254; Tert. Vert., p. 651.

is from the Wahsatch of New Mexico. It is about the size of the larger specimens of H. index. The first lower premolar is single rooted, and separated by a considerable diastema from the second. The third premolar has a very small second anterior cusp, and the fourth cusp on the last or fourth premolar is rather distinct. (Nos. 157a, 165, 4582 and 4603 of the Am. Museum collections.) One specimen in the collection (No. 165) shows a very decided variation, upon which I hesitate to propose a new species. The diastema between the first and second lower premolars is practically absent, and there is a well-developed second anterior cusp upon the third lower premolar. The first premolar is one-rooted, and the fourth has a very small fourth cusp. Several other species have been referred here by Cope, notably P. loevi and P. cinctus. The former of these I regard as a small variety of cristonense, and the latter I consider to belong to Orohippus, since it is from the Bridger formation.

Hyracotherium (Pliolophus) montanum, sp. nov.

I propose this species upon two fragments of lower jaws (No. 4593) of the same individual. The distinguishing character of this species is (1) the absence of any diastema between the first and second premolars, and (2) the two-rooted condition of the

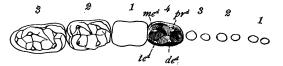


Fig. 13. Hyracotherium (Pliolophus) montanum. Lower teeth, crown view (type specimen, No. 4593). Wahsatch Beds, Big Horn. X §.

first premolar. In the specimen here described the crowns of the three anterior premolars are not preserved, but the roots indicate the characters mentioned above. The fourth premolar displays a small but distinct fourth cusp. The last two molars which are preserved exhibit the same structure as those in H. index, with the larger of which the present specimen agrees in size.

Protorohippus, gen. nov.

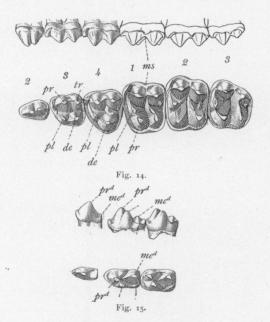
I come lastly to consider the Wind River representative of the horse family, which led directly up to the later Bridger form *Orohippus (Pachynolophus)*. The *generic characters* have already been referred to above, but may now be more definitely stated as follows: No vestige of the fifth digit in the hind foot. Superior molars with subcrescentic external cusps, and having frequently small but distinct rudiments of mesostyle and hypostyle. Fourth superior premolar with only three principal cusps, the fourth (antero-internal in this case) small and more or less in the position of an intermediate. Third superior premolar with four principal cusps, the antero-internal considerably enlarged and shifted inwards to form a cusp analogous with the protocone of the true molars.

By giving to this form a separate generic name we have a distinct genus for each of the groups of species in the four great divisions of the Eocene, as represented in this country, viz. : *Hyracotherium* in the Wahsatch, *Protorohippus* in the Wind River, *Orohippus* in the Bridger, and *Epihippus* in the Uinta.

Of these, Hyracotherium is the oldest and clearly the most primitive ; this is seen in the vestige of the fifth digit in the hind foot, the low conic form of the outer cusps of the superior molars, without any trace of the mesostyle or hypostyle, as well as the simple premolars. This is followed by Protorohippus, which has made a distinct advance in the loss of the vestige of the fifth digit in the hind foot, as well as the advance in the structure of both molars and premolars. Orohippus (Pachynolophus) continues the phylum into the Bridger, where the *third* and *fourth* premolars become fully molariform. This is again closely followed by Epihippus of the Uinta, in which the second superior premolar has assumed the molariform pattern, while from this latter genus to Mesohippus of the White River Miocene is but a short step, the only difference between the two which I am able to distinguish with certainty being the more perfectly molariform structure of the second superior premolar, and the reduction of the fifth digit of the fore foot to a vestige in the White River genus.

Protorohippus venticolus (Cope).

The type of this species is the more or less perfect skeleton described by Cope as *Hyracotherium venticolum* (No. 4832). The specific characters have been so fully stated by this author that I am unable to add anything to his original description. The



Figs. 14 and 15. Protorohippus venticolus.

Fig. 14. Upper teeth, side and crown views (composition from Nos. 4839 and 4832). Wind River Beds. $X_{\frac{4}{3}}$. Fig. 15. Lower premolars, side and crown views (No. 4834). Wind River Beds. $X_{\frac{4}{3}}$.

teeth of the type specimen are badly worn, and without additional material it would have been impossible to make out those important characters of the teeth, which in my judgment take it out of the genus *Hyracotherium*. A number of smaller specimens from the Wind River Beds (Nos. 4833-41) display the same characters as the type of the genus, but I hesitate to group them into a distinct species until more is known of them.

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PRINCIPLES OF PREMOLAR EVOLUTION IN THE AMERICAN HORSES.

A scheme of nomenclature for the cusps of the premolars has been proposed by Prof. W. B. Scott¹ for all the mammalia, in which it is attempted to express the homologies of the several parts of the tooth crown in all forms. Owing to some differences in the order of appearance of the several cusps in the different

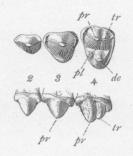


Fig. 16. Euprotogonia puercensis. Upper premolars, crown and side views (No. 3874). Puerco Beds of New Mexico. X $^4_3.$

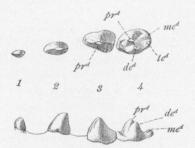


Fig. 17. *Euprotogonia plicifera*. Lower premolars, crown and side views (No. 4084). Puerco Beds of New Mexico. X ⁴/₃.

premolars, he selects the fourth as being constant in the manner in which the successive parts have been added. He says,² " so far as I have been able to observe, the scheme of development of the premolar crown is quite constant, and for superior premolar 4 universally so, and the nomenclature which is here

¹ Proc. Acad. Nat. Sci. Phila., 1892, p. 405. ² Loc. cit., p. 414.

proposed for the premolar cusps is intended to express their order of succession as they appear in this tooth."

The crown of the premolar in either jaw in its most primitive stage, consists of a single cone implanted by a single root; to this is added a second cusp, sometimes, as in the *superior series* of *Euprotogonia*, to the *inner* or lingual side of the primitive cone, and sometimes, as in *Hyracotherium index* and *Systemodon primævus*, immediately *posterior* to the primitive cone. The third element always makes its appearance either as this posterior cusp just mentioned (*Euprotogonia*), or as the internal cusp (*Hyracotherium*). In this stage of development we have therefore a three-cusped tooth with a triangular crown.

The primitive cone always occupies the same position, viz.: at the antero-external angle of the crown, and is known as the *protocone*. The cusp which is added to the lingual side of this cusp, irrespective of whether it appears previous to or subsequent to the posterior cusp, is given by Scott the name of *deuterocone*. In like manner the third cusp is called the *tritocone*.

In regard to the further complication of the tooth crown by which the tooth passes from a tritubercular to a quadritubercular stage, Prof. Scott further says : "The final step in the conversion of the premolar to the molar pattern is given by the addition of a fourth main element at the postero-internal angle of the crown, the *tetartocone*, which corresponds in position to the hypocone of the molars." Examples of this addition are to be seen in many forms, and it has undoubtedly been the usual method in the evolution of these teeth.

In the horse series of America, however, the addition of this fourth main element to the crowns of the superior premolars has pursued an entirely different course, and instead of appearing at the postero-internal angle of the crown, *it has been added at the antero-internal angle*. The proof of this assertion is to be found in the third and fourth superior premolars of *Hyracotherium index* and *Protorohippus venticolus*.

In the former of these species the crown of the fourth premolar is made up of two strong subequal more or less conic external cusps, together with a large simple median more or less lunate internal cusp. A little anterior and internal to this cusp, as if it

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were a slightly constricted off part of the large crescentic internal, is a small cusp, occupying the position of an intermediate or protoconule. In the third premolar this same cusp is to be seen, but it is stronger and has a more forward position, giving to the crown a more quadrangular outline.

In *Protorohippus venticolus* this cusp in the crown of the third premolar is decidedly stronger, and has such a forward and internal or lingual position as to give to the crown quite a quadritubercular appearance. In the fourth premolar the position of this cusp is more nearly as it is in the third premolar of *H.index*, and the crown has not made as rapid progress towards the quadritubercular condition as the third. It has, however, made considerable advance in the direction of the formation of the anterointernal cusp, as is seen in the more forward and inward position of the element which is destined to become the fourth tubercle.

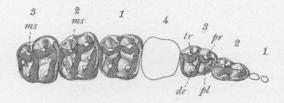


Fig. 18. Orohippus, sp. Upper teeth, crown view (composition.from Nos. 1735, 1737 and 1738). Bridger Beds, Wyoming. X $\frac{4}{3}$.

In the Bridger species of *Orohippus* a still further advance is made, and both third and fourth premolars have become almost fully molariform or quadritubercular by the still greater enlargement and growing inwards of this cusp under consideration.

It is thus demonstrated, I hold, that the antero-internal cusp in these premolars was the last of the principal elements added, and while it is analogous, so far as the date of its appearance is concerned, with the *tetartocone* in other forms, it is not homologous with the cusp so named, either in position or in origin.

Another fact of much interest in this connection is the practical assumption of the molariform structure of the third superior premolar in advance of the fourth in the American Horses. This is apparently not true of the European species, if one can place any dependence upon the drawings of Kowalewsky and Rütimeyer, nor, on the other hand, is it true that the antero-internal cusp was the last one to be added to complete the quadritubercular crown in the European species, as I have attempted to show above is true of the American species. Upon this ground I hold that the Lower Eocene European and American Horses probably represent entirely distinct phyla, having in all probability a common beginning in the least modified species of the genus *Hyracotherium*.

EXPLANATION OF PLATE II.

UPPER AND LOWER TEETH OF EOCENE HORSES.

A-E. Upper teeth. All natural size.

- A. Euprotogonia puercensis, No. 3874, Puerco Beds, New Mexico.
- B. Hyracotherium tapirinum, Nos. 139, 212, Wahsatch Beds, Big Horn.
- C. " index, No. 4602, Wahsatch Beds, Big Horn.
- D. Protorohippus venticolus, Nos. 4839, 4832, Wind River Beds.
- E. Orohippus sp., Nos. 1735, 1737 and 1738, Bridger Beds.
- F-N. Lower teeth. All natural size.
 - F. Euprotogonia plicifera, No. 4084, Puerco Beds, New Mexico.

| G. | Hyracotherium | vasacciense, | No. 4659, | Wahsatch | Beds, | Big Horn. | |
|----|---------------|--------------|-----------|----------|-------|-----------|--|
| | | | | | | | |

| ч. | Tyraconcertain bacaconcert, 110: 4059; Wansaten Beds, Big Hom. | | | | | |
|------------|--|--|------------------------------|--------------------|--------------------------|---------|
| Н. | " | cristatum, N | Nos. 240, 258 | в, " | | |
| Ι. | " | (Pliolophus) | cristonense, | No. 165, Big Ho | | Beds, |
| Ι'. | " " | " | | | Nat. Mus. lew Mexico. | Coll.), |
| <i>J</i> . | | " | <i>montanum</i> , Big Hor | | , Wahsatch | Beds, |
| K. | | tapirinum, Nos. 143a, 4657, Wahsatch Beds, Big Horn. | | | | |
| L. | " " | index, No. 4613, Wahsatch Beds, Big Horn. | | | | |
| М. | 6 6 | craspedotum, No. 4830, Wind River Beds. | | | | |
| N. | Protorohippus | venticolus, N | 0. 4834, | ** ** | " | |

ABBREVIATIONS: pr.=protocone, me.=metacone, pa.=paracone, de.=deuterocone, tr.=tritocone, hy.=hypocone, pl.=protoconule, ms.=metastyle, prd.=protoconid, pad.=paraconid, med.=metaconid, hyd.=hypoconid, ded.=deuteroconid, $te^{d.}=$ tetartoconid, $ps^{d}=$ parastylid, $hl^{d.}=$ hypoconulid.

