Article XII. — PERISSODACTYLS OF THE LOWER MIocene WHITE RIVER BEDS.

By Henry Fairfield Osborn and J. L. Wortman.

With Plates VIII-XI and twelve Figures in the Text.

INTRODUCTION.

The progress of our knowledge of the White River fossil fauna has been extremely rapid since 1892, owing chiefly to the discovery of the 'Protoceras Beds,' the location of the 'Metamynodon level,' and the very exact stratigraphic and expert collecting methods employed by the American Museum and Princeton exploring parties.

The most welcome result of the field work is that we are now securing complete skeletons of animals which have been hitherto represented only by isolated skulls and limbs. We can now replace the useful but largely conjectural 'restorations' of the last decade by figures taken directly from the skeletons. The two types illustrated in this Bulletin are the massive Titanotherium, and the smaller but no less interesting Metamynodon, drawn from complete skeletons which have recently been mounted by Mr. Hermann for the new hall of Vertebrate Palæontology.

The second result, less striking perhaps, but of equal importance, is that we are obtaining very much more perfect and abundant examples of the rarer forms of White River Mammals.

The present paper is confined to the publication of new or little known characters of the Perissodactyla, and includes the following points of chief interest:

1. The entire skeleton of Titanotherium robustum is described. The vertebral formula is shown to differ from that of all other Perissodactyla, and to agree with that of the Artiodactyla. It is probable that certain wide differences in the development of the
horns, which have been assigned a generic value, are merely sexual characters.

2. The White River Horses exhibit a very marked evolution in size as we pass from the lower to the upper White River levels. There is apparently a direct specific succession connecting *Mesophippus bairdi* Leidy, through *M. intermedius* (nobis) of the 'Protoceras Beds,' with *Anchitherium prestant* Cope of the John Day Beds. A distinct, very much larger, and apparently new type of Horse is the *M. copei* of the Protoceras Beds.

We have thus in the horse line reached the point long ago predicted by Lamarck in promulgating the evolution theory, namely, that the lines drawn in the Linnaean system of nomenclature would be finally obliterated by discovery. In fact we are now beginning to retain the binomial system upon grounds of convenience and of scientific courtesy, rather than upon lines of definition.

3. The true Lophiodontidae of Europe are found to be represented in this country by the *Heptodon-Helaletes-Colodon* line previously referred by Marsh and ourselves to the Helaletidae. The alleged *Hyrachus douvillei* of Filhol is actually identical with *Colodon*, showing that a contemporary transformation of the *Lophiodons* occurred in Europe and in this country. The peculiar foot formerly referred by us to *Mesophippus longipes* now appears to belong to a member of this phylum.

4. The differences between the Tapir, Lophiodon and Hyrachyus molar types are clearly defined.

5. The skull of *Hyrachyus agrarius* from the Bridger Beds is described in this connection.

6. The mounted skeleton of *Metamynodon planifrons* is described.
The stratigraphical position of the species described in this Bulletin is shown in the following table:

<table>
<thead>
<tr>
<th>JOHN DAY BEDS, OREGON.</th>
<th>GEOLOGICAL SUCCESSION.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approximate estimate of the thickness of the Beds.</td>
<td>The stratigraphical position of the species described in this Bulletin is shown in the following table:</td>
</tr>
<tr>
<td>PROTERAS BEDS.</td>
<td>Acatherium tridactyllum, A. playfordi, Metoposaurus intermedius, Mesophippus roset.</td>
</tr>
<tr>
<td>Protoceras Clays. 100 feet.</td>
<td>Leptocystena Layer: nodules-bearing,</td>
</tr>
<tr>
<td></td>
<td>Oreodon beds. 50-75 feet.</td>
</tr>
<tr>
<td></td>
<td>Oreodon Layer: sandstones and clays.</td>
</tr>
<tr>
<td>OREODON BEDS. 75 to 100 feet.</td>
<td></td>
</tr>
<tr>
<td>10 to 20 feet.</td>
<td></td>
</tr>
<tr>
<td>50 feet.</td>
<td></td>
</tr>
<tr>
<td>TITANOTHERIUM BEDS.</td>
<td></td>
</tr>
</tbody>
</table>
Family TITANOTHERIIDÆ.

Genus Titanotherium Leidy.

Titanotherium robustum Marsh.

Plates VIII and IX.

The chief result of the Museum Expedition of 1892, under Dr. Wortman, assisted by Mr. O. A. Peterson, was the discovery of a large Titanotherium skeleton (No. 518) in the upper Titanotherium beds of South Dakota near the head of Corral Cañon. The skull was first found, in a somewhat shattered condition, and then the neck, entire trunk and fore limbs, perfect even to the sesamoids, were excavated as far back as the last lumbar vertebra and the border of one ilium. At this point, to their great disappointment, the party encountered a sudden change in the rock, and found that the sacrum, remainder of the pelvis and hind limbs had been carried away by an erosion which had probably occurred some time after the original deposition of the entire animal. A vigorous search in the summer of 1894 for hind limbs of the proper proportions resulted only in the finding of a left tibia (No. 1075) and fibula (No. 1071), and a left pes (No. 1073), left calcaneum and astragalus (No. 1076). Finally, by the kind cooperation of the Princeton parties under Mr. Hatcher and Mr. J. W. Gidley, the Museum secured a perfect pelvis (No. 1065) and two femora (Nos. 1442, 1443) belonging to three different individuals. The size of these parts was determined (1) by the fact that the pelvis corresponds very closely to that belonging to the main skeleton; (2) one of the femora had associated with it metacarpal bones, which also agree in size with those of the main skeleton. We thus have every reason to believe that the proportions between the fore and hind limbs are very nearly accurate.

The entire animal was then put together and mounted with the greatest skill by Mr. Adam Hermann, head preparator of the Department of Vertebrate Palæontology. The only parts which he found it necessary to restore were the teeth of the left side and certain smaller gaps in the skull; the sacrum and a few of the
caudals; the cuboid, navicular and cuneiforms of the left pes; part of the right tibia (No. 493), calcaneum (1073), and the major part of the right pes. These missing parts were carefully modeled from the opposite side or from other individuals of different size. The only parts missing are the manubrium sterni and some of the posterior sternals.

The completed skeleton is about 14 feet long, 8 feet high and 4 feet broad. The teeth are well worn, yet the epiphyses upon the summits of the dorsals indicate that the animal was not fully adult. An interesting feature of the skeleton is the exostosis and false joint in the center of the seventh rib, undoubtedly an after result of fracture.

The skeleton differs from the Scott-Osborn restoration of Titanotherium proutii (Fig. 2) mainly because T. proutii is a more primitive and less robust type. Marsh's restoration of T. (Brontops) robustum, executed by Mr. Berger, is a remarkably

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skillful drawing of the trunk and limbs, but errs in the too small proportions of the skull, as seen by a comparison with our Fig. 1, a perspective drawing by Mr. Weber. The Scott-Osborn and Marsh restorations are both at fault, however, in placing too many vertebrae in the dorso-lumbar series. This animal actually possessed but twenty dorso-lumbars.

Fig. 2. *Titanotherium proutii*. As restored in 1887 by Scott and Osborn; now modified by reduction of the lumbars. One-thirty-second natural size.

**SEXUAL AND SPECIFIC CHARACTERS.**

This animal was found in the same level (Upper Titanotherium Beds), and agrees closely in size and appearance with the type skeleton of *Titanotherium (Brontops) robustum* of Marsh.¹ The cheek teeth characters (pm.=4, m.=3) are also the same. In the American Museum specimen the premaxillaries are imperfect, and we cannot determine the number of incisors in either jaw. In Marsh’s type there are two upper incisors. In the Museum collection there is also a fine skull (No. 492) with a very

long pair of horns. This agrees closely with Marsh's type of *T. (Titanops) elatum*. It is noteworthy that the alleged distinct species, *T. robustum* and *T. elatum*, and the American Museum specimens similar to them, both occur upon the same level, and were therefore contemporaneous. They agree in the length of the nasals, in many minor details of skull structure, and in the characters of the dentition. They differ mainly in the size of the horns, a character which is very generally of sexual significance only. The conclusion appears very probable that the genus and species *Titanops elatus* is founded upon a male individual of the genus and species *Brontops robustus*, the latter having been established upon a female individual.

The species *T. robustum* appears to differ somewhat from the previously established *T. dolichoceras* Scott and Osborn, in the flatter horn section and longer nasals, but it may subsequently appear that these differences are not of specific value.

**Dimensions of Skeleton.**

<table>
<thead>
<tr>
<th></th>
<th>Feet</th>
<th>Inches</th>
<th>Metres</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length, tips of nasals to bend of tail</td>
<td>13</td>
<td>8</td>
<td>4.15</td>
</tr>
<tr>
<td>Height</td>
<td>7</td>
<td>7</td>
<td>2.30</td>
</tr>
<tr>
<td>Breadth, across pelvis</td>
<td>3</td>
<td>10</td>
<td>1.18</td>
</tr>
<tr>
<td>Hind limb, total length</td>
<td>5</td>
<td>6</td>
<td>1.67</td>
</tr>
<tr>
<td>Femur, &quot; &quot;</td>
<td>2</td>
<td>7</td>
<td>.79</td>
</tr>
<tr>
<td>Tibia, &quot; &quot;</td>
<td>1</td>
<td>4½</td>
<td>.42</td>
</tr>
<tr>
<td>Metatarsal III, length</td>
<td>8</td>
<td></td>
<td>.205</td>
</tr>
<tr>
<td>Fore limb, total length, including scapula</td>
<td>6</td>
<td>9</td>
<td>2.05</td>
</tr>
<tr>
<td>Scapula</td>
<td>2</td>
<td>2½</td>
<td>.67</td>
</tr>
<tr>
<td>Humerus</td>
<td>1</td>
<td>9½</td>
<td>.55</td>
</tr>
<tr>
<td>Radius</td>
<td>1</td>
<td>6</td>
<td>.46</td>
</tr>
<tr>
<td>Ulna, including olecranon</td>
<td>1</td>
<td>11½</td>
<td>.60</td>
</tr>
<tr>
<td>Metacarpal III, length</td>
<td>9</td>
<td></td>
<td>.23</td>
</tr>
<tr>
<td>Skull, length, incisors to condyles</td>
<td>2</td>
<td>7½</td>
<td>.80</td>
</tr>
<tr>
<td>Molars, Premolars, Canine inclusive</td>
<td>1</td>
<td>5</td>
<td>.45</td>
</tr>
<tr>
<td>Vertebral column, total length, excluding caudals, (including intervertebral spaces)</td>
<td>9</td>
<td>3½</td>
<td>.71</td>
</tr>
<tr>
<td>7 Cervicals, total, inferior centra</td>
<td>2</td>
<td>4</td>
<td>1.65</td>
</tr>
<tr>
<td>17 Dorsals, &quot; &quot;</td>
<td>5</td>
<td>5</td>
<td>.28</td>
</tr>
<tr>
<td>3 Lumbars, &quot; &quot;</td>
<td>1</td>
<td></td>
<td>.19</td>
</tr>
<tr>
<td>4 Sacrals, &quot; (estimated)&quot;</td>
<td>3</td>
<td>9½</td>
<td>1.15</td>
</tr>
<tr>
<td>20 Caudals, &quot; &quot;</td>
<td>2</td>
<td>3½</td>
<td>.70</td>
</tr>
<tr>
<td>4th Dorsal Vertebra, length, with spine</td>
<td>3</td>
<td>2</td>
<td>.96</td>
</tr>
<tr>
<td>5th Rib, length, outer measure</td>
<td>3</td>
<td>7½</td>
<td>1.11</td>
</tr>
</tbody>
</table>

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1 Osborn and Wortman, *Perissodactyls of White River*. 349
The most characteristic features of the animal are the following:

*Skull.*—The nasals are of medium length; the horns are short, forwardly projecting, and imperfectly ossified at the tips. The zygomatic portion of the squamosal shows a decided posterior bulge but no shelf-like projection. The supra-occipital border is deeply indented.

*Vertebrae.*—The fine series of vertebrae belonging to No. 518, complete to the last lumbar but lacking the sacrals and caudals, enables us to fully describe and illustrate the backbone. The plate (Pl. IX) is taken from an enlarged drawing made just after the vertebrae were mounted. The exceptional number of dorso-lumbar vertebrae suggests the note that a fracture was found through the center of the first lumbar, but there is no probability that one of the lumbers is missing. The formula is:

Cervicals, 7; dorsals, 17; lumbers, 3; sacrals, 4.

The number of dorso-lumbars therefore coincides with that in the Artiodactyla, namely, D.L. = 20, and is from three to four less than that typical of the Perissodactyla, namely, D.L. = 23-4. This corroborates a view already advanced by Osborn,¹ that of all Perissodactyla the Titanotheres present the greatest number of affinities to the Artiodactyla; these affinities may now be summarized as follows: the artiodactyl type of fore foot, the artiodactyl type of superior molars, the vertebral formula characteristic of the Artiodactyla. It is premature to infer more from these facts than that if the Artiodactyla and Perissodactyla were derived from a common stem form, as expressed in the larger division Diplarthra of Cope, the Titanotheres have diverged less from this stem than other Perissodactyla, at least in the development of the above-mentioned characters. It is possible also that the shortening of the backbone may be secondary, so that the above generalization requires further verification by the discovery of the vertebral formula in the ancestral Titanotheres.

In details the vertebrae show many resemblances to those of *Palaeosyops paludosus,* as described by Earle. The atlas has a broad powerful transverse process with an inferior flange pierced by the vertebrarterial canal; the suboccipital nerve issued just above the anterior border of the process. The axis has a peg-like

¹ 'Rise of the Mammalia in North America,' p. 34.
odontoid and a powerful spine. The cervicals 3–6 are characterized by a progressive increase in the height of the neural spine, in the size of the transverse process and extension and depression of its inferior lamella; the post-zygapophyses are flat, similar in shape, and face downwards and outwards. The 7th cervical is imperforate with a greatly reduced transverse process. The dorsals are characterized by the sudden elevation, in d. 1–4, and gradual sinking of the spines as we pass backwards. Every dorsal from d. 1–17 is characterized by a facet for both the head and tubercle of the corresponding rib. The zygapophysial facets lie in a nearly horizontal plane from d. 1 to d. 11; they then gradually shift to an oblique plane from d. 12 to d. 14; and into a nearly vertical plane in d. 15–16. The zygapophyses of the 17th dorsal and 1st lumbar vertebrae are distinguished from all the others by being slightly concavo-convex. The post-zygapophysis of the 2d lumbar is plane and slightly oblique in position. The lumbar metapophy-
ses are flat and horizontal. The 3d lumbar articulates by an oblique facet and broad metaphyseal process with the 1st sacral. The sacrum is unfortunately missing. Marsh states that there are four in this species. We find four in the perfectly preserved pelvis (No. 492) associated with the supposed male skull. The caudals are from a number of different individuals. The neural spines apparently extend back to the 8th vertebrae. The transverse processes die out upon the 6th. A well-developed chevron appears upon the 2d, and perhaps in a perfect series would be found upon the 3d.

Fore Limb.—The fore limb is of an extremely robust character. The scapula shows a projection of the anterior border, a rounded and rugose superior border, and a long incurved posterior border. The most striking bone is the humerus with its huge plate-like great tuberosity, strong deltoid ridge, and powerful ectocondylar ridge. The shaft of the ulna is trihedral in section and stands well out from that of the radius. The radius has a flattened shaft and a well-marked inferior extensor groove. The structure of the manus is typically paraxonic or artiodactyl, the median axis of the foot lying between the third and fourth digits. Other features of the skeleton are well illustrated in the drawings.

Family EQUIDÆ.

Subfamily ANCHITHERIINÆ.

Genus Mesohippus Marsh.

Representatives of this genus are exceedingly abundant in the White River formation, and as a result of the several expeditions made by the Museum party into these beds an unusually fine series of Horses of this epoch is contained in the collection. Several definitions of the genus have been given, the latest of which is by Scott, in which he assigns the presence or absence of the enamel pit in the superior incisors to distinguish it from the John Day Horses, which he places under the generic title of Miohippus. He ascribes to Mesohippus complete absence of any enamel invagination in the upper incisors, but adds in a footnote,

“The upper incisors of this genus are not known, and future discovery may show that it is not generically different from *Mio-hippus*, but the generally less advanced character of the dentition renders it probable that the character of the incisors is as assumed above.”

There are in our collections two specimens in which the superior incisors are preserved in an almost perfect condition; they both show a very decided pitting of the enamel in the two outer teeth. It will therefore be readily seen that the generic distinction between the White River and John Day species fails, and we really know of no characters of generic value by which they can be distinguished. In a like manner the distinctions between *Mesohippus* and *Anchitherium* disappear when one examines carefully a large series of White River and John Day Horses.

Previous to the discovery of the Protoceras fauna in the upper part of the White River beds, but a single species, *M. bairdii*, had been generally recognized in this formation, but with the acquisition of a large amount of material from the upper level it is now possible to demonstrate that there were two and probably three species living in that region when the successive sediments were laid down.

**Synopsis of Species of Mesohippus.**

*M. bairdii.*

1. Median pair of incisors not cupped.
2. Length of median metapodial of fore-foot, .080—.095.
3. Length of median metapodial of hind-foot, .107—.124.
4. Parastyle of Sup. Pm. 2, small.
5. Intermediate cusps of Sup. Ms. and Pms. little separated from internal cusps.

*M. intermedius.*

1. Median pair of incisors slightly cupped.
2. Length of median metapodial of fore-foot, .130—.132.
3. Length of median metapodial of hind-foot, .151—.152.
4. Parastyle of Sup. Pm. 2, enlarged.
5. Intermediate cusps same as in *M. bairdii*.

*M. copei.*

1. Unknown.
2. Unknown.
3. Length of median metapodial of hind-foot, .189.
4. Parastyle of Sup. Pm. 2, slightly enlarged.
5. Intermediate cusps of Sup. Ms. and Pms. well separated from internal cusps.

1 Several species have been proposed for remains from this horizon, but it seems probable from the descriptions that they pertain only to individual varieties of the most prevalent species *M. bairdii*. Marsh has described *M. celer*, and Cope has described *M. cuneatum* and *M. exoletum* from the Miocene of Colorado.
2 These characters are taken from the second specimen, No. 683.
Mesohippus intermedius, sp. nov.

This species is based upon an almost complete skeleton (No. 1196) from the sandstones of the Protoceras layer of White River. There are, moreover, numerous other specimens including perfect feet, skulls, jaws and other parts of the skeleton from the same layer of both the White and Cheyenne River localities contained in the collection.

These specimens all agree very closely in size, and average nearly one-third larger than M. bairdii from the lower or Oreodon layer. A comparison of the length of the median metapodials in different individuals is as follows:

<table>
<thead>
<tr>
<th>M. bairdii</th>
<th>M. intermedius</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of median metapodial, hind foot</td>
<td>.107</td>
</tr>
<tr>
<td></td>
<td>.114</td>
</tr>
<tr>
<td></td>
<td>.117</td>
</tr>
<tr>
<td></td>
<td>.124</td>
</tr>
<tr>
<td>Length of median metapodial, fore foot</td>
<td>.080</td>
</tr>
<tr>
<td></td>
<td>.095</td>
</tr>
</tbody>
</table>

It will be seen from this table that there is marked increase in the size and length of the metapodials of M. bairdii, and it is interesting to note that the smallest examples of the species in our collection at least come from the lower layers, while the largest examples were found in the highest levels of the Oreodon stratum.

Not only do our specimens of M. bairdii show great variation in size, but marked individual variability in important structural characters as well. Fully fifty per cent. of the specimens show coössification of the three cuneiforms into a single bone; others have the middle and internal cuneiforms united, while others again have all three bones free. The degree of reduction of the lateral metapodials is subject to much variation, as is also the extent of the development of the metapodial keels. The teeth vary greatly in the details of their structure, some showing much greater advancement than others.

In M. intermedius the variation is apparently not so great, especially as regards size. In some specimens the metapodials
are thicker and stouter, the lateral ones being subcircular in section near the middle, while in other specimens the metapodials are decidedly more slender, the lateral ones being highly compressed laterally and very elliptical in cross section. In contrast

![Diagram of animal feet]

with *M. bairdii* the arrangement of the cuneiform bones seems to be very constant; the middle and internal are always united, while the external is free.

Another important distinction between *M. bairdii* and *M. intermedius* is seen in the degree of the cupping of the incisors. In *M. bairdii* the two outer incisors are very distinctly cupped,
but the median pair show no traces whatever of the enamel pit. In \textit{M. intermedius}, on the other hand, the median pair are slightly but distinctly cupped. In this respect the incisors of \textit{M. intermedius} stand exactly half-way between those of \textit{M. bairdii} and the John Day species, \textit{Anchitherium preestans}, in which the median incisors are always distinctly and almost as strongly cupped as the two outer ones.

In the superior premolar dentition there are also important differences which point strongly in the direction of the John Day species, especially \textit{Anchitherium preestans}. In \textit{M. bairdii} the internal cingulum of the first superior premolar is but little developed, and does not form with the principal cusp a distinct basin; in \textit{M. intermedius} the cingulum is more strongly developed and a distinct basin is formed.

In the second superior premolar of \textit{M. bairdii} the parastyle or cingular cusp at the antero-external angle of the crown is small and scarcely larger than those on the succeeding teeth. In \textit{M. intermedius} this cusp of the second premolar is considerably enlarged, giving to the crown an incipient triangular appearance. In \textit{Anchitherium preestans} the enlargement of this cusp is carried still further, and in \textit{Protohippus} and \textit{Equus} the crown of the tooth is of a triangular shape in front.

The chief distinctions between \textit{M. intermedius} and \textit{Anchitherium preestans} are seen in the cupping of the median pair of incisors, the greater enlargement of the parastyle of the second superior premolar, the union of the posterior cross-crest with the outer wall in the superior molars and premolars, the greater reduction of the lateral metapodials, and the larger size of the latter species.

\textbf{Mesohippus copei}, sp. nov.

This species is founded upon the complete half of a pelvis, femur, tibia, and part of a hind foot (No. 1197), together with a complete median metapodial, and one lateral metapodial of the hind foot of another individual (No. 1198), a collateral type. These remains indicate an animal much larger than \textit{M. intermedius}, and this is, so far as we know, the largest horse of the White River epoch, larger even than \textit{A. preestans} of the John
Day. A comparison of the measurements of these bones with those of *M. intermedius* is as follows:

<table>
<thead>
<tr>
<th></th>
<th><em>M. copei</em></th>
<th><em>M. intermedius</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of tibia</td>
<td>.317</td>
<td>.240</td>
</tr>
<tr>
<td>Width of astragalus</td>
<td>.041</td>
<td>.035</td>
</tr>
<tr>
<td>Length</td>
<td>.048</td>
<td>.041</td>
</tr>
<tr>
<td>Length of middle metapodial of hind foot</td>
<td>.189</td>
<td>.151</td>
</tr>
<tr>
<td>Length of pelvis</td>
<td>.334</td>
<td></td>
</tr>
<tr>
<td>Width</td>
<td>.231</td>
<td></td>
</tr>
</tbody>
</table>

There are also in our collection two superior premolars (No. 683) of the right side, apparently the second and third of the series, that are much larger than any specimens of *M. intermedius*. We have therefore provisionally referred these teeth to this species. If this reference is correct, these teeth indicate a species quite different structurally from *M. intermedius*. Besides their greater size, the intermediate cusps are much more distinct, being separated from the internal cusps by a wide, deep notch, whereas in *M. intermedius* they form with the internal cusps a high crest and are very little separated.

The measurements of these premolars are as follows:

<table>
<thead>
<tr>
<th></th>
<th><em>M. copei</em></th>
<th><em>M. intermedius</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of second and third superior premolars</td>
<td>.037</td>
<td>.030</td>
</tr>
<tr>
<td>Width of second premolar</td>
<td>.018</td>
<td>.015</td>
</tr>
<tr>
<td>Width of third premolar</td>
<td>.021</td>
<td>.017</td>
</tr>
</tbody>
</table>

This species differs from *Anchitherium prastans* in the less reduced character of the lateral metapodials, and in the lack of completion of the cross-crests of the superior premolars, as well as the distinctness of the intermediate cusps. The two species are nearly equal in size.

All of our material is from the Protoceras layer of the Cheyenne River locality, but a large foot, probably of this species, was found by Mr. J. B. Hatcher, of the Princeton expedition, in the Oreodon Beds.
The above table represents the nearly continuous sedimentation from the Titanotherium Beds into the John Day, having a total thickness of about eight hundred feet.

There can be little doubt that the three types, *Mesohippus bairdii*, *M. intermedius* and *A. prastans*, form a distinct and closely connected phylogenetic series of animals slowly specializing and constantly increasing in size. So far as we know there is not a single character missing in the structural chain. *Mesohippus* or *Anchitherium copei*, on the other hand, is somewhat larger than *A. prastans*, and forms a side branch, leading possibly into one of the numerous parallel species which Cope and Scott have described from the John Day and Deep River Beds.

**Family LOPHIODONTIDÆ.**

*(Sensu strictu.)*

A family of lophodont Perissodactyls intermediate between the Tapiridae and Hyracodontidae. Superior molars, with paracone and metacone of same size but differing in shape. Metacone pushed inwards, more or less concave. Paracone lengthened. Metacone shortened.

**Heptodon.**

Incisors 3, premolars 4, 4. Third and fourth superior premolars without posterior crests. Digits 4-3 Median toes enlarged.

**Lophiodon.**

Incisors 3, premolars 4, 4. Third and fourth superior premolars without posterior crests. Manus and pes unknown.

**Helaeletes.**

Incisors 3, premolars 4. Third and fourth superior premolars with posterior crests.

**Colodon.**

It now proves that Leidy was very near the truth in referring to Cuvier's genus _Lophiodon_ certain Bridger (_L. nanum_) and White River (_L. occidentalis_) jaws and teeth. The discovery of the superior molar series of _Colodon_ demonstrates beyond a doubt that true Lophiodontidae, not in the loose sense of the term of Cope, Lydekker and Flower, but in the strict phylogenetic or true relationship sense, were represented in North America by the animals hitherto grouped in the family Helaletidae by Marsh and Osborn. This family identity has been anticipated by Osborn.² The true American Lophiodonts are now seen to be

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1. *Mammals, Living and Extinct,* 1891, p. 373. By these authors, *Hyracotherium, Systemodon, Hyrachyus,* in fact all lophiodont Perissodactyls in which the premolars are simpler than the molars, are termed 'Lophiodonts' without regard to the wide gaps which separate them from the true _Lophiodon_.

Heptodon of our Wahsatch, Helalates of the Bridger and Uinta, and Colodon of the White River. It now appears that besides Lophiodon, both Helalates and Colodon probably occur in Europe as the last representatives of the Lophiodon line.

Cuvier's type, L. tapiroides, is a lower jaw found at Issel, an horizon which contains Pachynolophus, and is approximately equivalent to our Bridger. The Bridger species of Helalates, namely: H. (Hyrachyus) nanus Leidy, H. boops Marsh, H. (Desmatotherium) guyotii S. & O., H. (Dilophodon) minusculus S. & O., are well known to differ from the Issel Lophiodons (L. tapiroides Cuvier, L. isselensis Fischer) in the possession of rudimentary transverse crests upon two superior premolars. In the higher White River horizon the species of Colodon, namely, C. occidentalis Leidy, C. (t) longipes O. & W., C. dakotensis O. & W., C. procuspidatus O. & W., differ still further from Lophiodon in the possession of posterior crests upon three of the upper premolars.

The true molar pattern in Heptodon, Lophiodon, Helalates and Colodon is identical; the question arises, can we separate the oldest American type, the Wind River or basal Bridger Heptodon, with its unmodified premolars, from Lophiodon? It now seems that we can do so. So far as we know, Cope's Heptodon is nearly identical with Cuvier's Lophiodon, the only distinction being one of size, and the number of upper premolars. The likeness is in the identical pattern of the molar teeth and the absence of posterior crests upon the premolars.

The skeleton of Heptodon, as previously shown by the writers, is highly specialized, resembling that of the Hyracodons in many respects, but tending still more to monodactylism. The climax of this tendency is shown in a White River hind-limb, which we at first referred to Mesohippus, but which now appears to belong to a form probably related to Colodon. The extremities of Lophiodon are not known, or have not been described. The nearest approach to the Heptodon type of skeleton in the French Eocene beds is that which has been referred to Palopotherium minus by the French palæontologists. The P. minus tarsus and hind limb are almost identical in size and in numerous minor characteristics

with the *Heptodon* limb. We do not know whether the association of the *P. minus* skeletal parts with the teeth of the *Paloplotherium* type is absolutely demonstrated; if it is not, it seems quite probable that the so-called *P. minus* feet belong not to the Palaeotheres (from which they differ so widely), but to some small Lophiodont such as *Heptodon*.

Genus **Heptodon** Cope.

For a full account of this Wind River type, see our paper upon the Wahsatch Fossil Mammals, and Prof. Cope’s description in the ‘Tertiary Vertebrata.’

Genus **Lophiodon** Cuvier.

Under this genus should be included only those forms with simple premolars which are *identical* in molar pattern with Cuvier’s type, such as *L. tapiroides* Cuvier, *L. isselensis* Fisher, *L. parisiense* Gervais, *L. buchsovillanum* Blainville.

We may confidently exclude all those European forms which have the true Tapir, Rhinoceros, Hyracodon or Amynodon molar pattern, and which undoubtedly belong to animals ancestral to *Cadurcotherium*, to *Protapirus*, to *Aceratherium*, and possibly to the Hyracodonts. This will remove from *Lophiodon* a host of wrongly-referred species.

The question, What is *Lophiodon*?\(^1\) seems now nearer solution. It is intermediate in molar pattern and in skeletal characters between the Tapirs and Hyracodonts or Rhinoceroses, and shows a mingling of their characters, but represents a line of descent entirely distinct from both.

Genus **Helaletes** Marsh.

For the synonymy and characteristics of this type, see Scott and Osborn’s Memoir upon ‘Mammalia of the Uinta Formation,’ our paper upon the Wahsatch Mammals,\(^2\) and Wortman and Earle’s paper upon ‘Ancestors of the Tapir from the Lower Mio- cene of Dakota.’\(^3\)

\(^1\) Osborn, American Naturalist, Sept., 1892, p. 763.
Genus *Colodon* Marsh.

There is no evidence that the true *Hyrachyus-Hyrrcodon* line existed in Europe; the *Colodon* genus or stage of Lophiodont development, is probably represented in France by the animal from St. Gérard de Puy, which Fihol has mistakenly referred to *Hyrachyus*,¹ as *H. douvillei*.

In our former communication upon the American representatives of this genus,² we had no hesitancy in referring it to the family Helaletidae from the North American Eocene, and regarding it as the probable successor of the Upper Eocene representative (*Helaletes*) of this family. Additional material, collected by the Museum Expedition of last year, now enables us to not only clear up the question of the species, but at the same time throws a new light upon the probable family relationship of these Tapiroids, as above detailed.

An analysis of the species may now be given as follows:

Size large; length of last two lower Ms. and last two lower Pms., .072.
Postero-internal cusp of the last lower premolar double. Internal cusps of superior premolars not fully distinct; no external nor internal cingula on premolars. .......... .......... *C. dakotensis*.

Size large; length of lower Pms. and Ms. unknown; last inferior premolar unknown. Internal cusps of second and third upper premolars distinct and well separated; an external and internal cingulum upon premolars .......... .......... *C. procuspidatus*.

Size small; length of last two Ms. and last two lower Pms., .055.

Previously established upon foot characteristics only, possibly equivalent to *C. dakotensis* .......... .......... .......... .......... *C. longipes*.

**Colodon dakotensis**, sp. nov.

The type of this species consists of an entire superior molar and premolar dentition lacking only the first premolar of the left side (No. 1212). To this we add as a collateral type a specimen of another individual displaying the second and third lower premolars, the second and third lower molars of the right side, and the fourth upper premolar of the left side (No. 1213).

¹ Annales des Sciences Geologiques, T. xvii, pl. vi, fig. 13.
The superior cheek teeth consist of four premolars and three molars. The first premolar is small, having a triangular crown with a single fully-developed external and internal cusp. The postero-external cusp (tritocone) is faintly indicated by a groove in the main external cusp, as is also the antero-internal (deuterocone) represented by a small but distinct tubercle situated just in advance of the large internal cusp.

The succeeding three premolars increase slightly in size from before backwards; their crowns are more or less quadrate in outline, and each displays a double external and internal cusp connected by well-defined cross-crests. The internal cusps of the premolars are not fully developed and distinct from each other in this species, but are indicated by a deep vertical groove upon the internal face of the crown. It is a matter of importance to note that in the assumption of the double internal cusps of the premolars, this species furnishes us with the incipient and transition stages, and further, that this complication began in the second premolar and proceeded backwards. This is demonstrated by the fact that the second premolar is more advanced in this respect than the third, and the third is more advanced than the fourth.

The arrangement of the external cusps is somewhat different from that of the true molars, in that the posterior external cusps of the premolars are not pressed inwards and concave as they
are in the molars. The parastyle at the antero-external angle of the crown is faintly but clearly indicated, and there can be said to be no external or internal cingula developed upon any of the premolars.

The structure of the true molars has already been described, and, so far as can be determined from the materials at hand, varies but very little in the different species. It is, however, worthy of remark that the cingulum in this species is but faintly if at all indicated upon any of the molars.

Of the inferior molar dentition the structure is very similar to that of *C. occidentale* in general appearance. An important structural difference between the species, however, is to be seen in the last inferior premolar; in *C. dakotensis* the posterior portion of the crown widens rapidly, and the postero-internal cusp is double, whereas in *C. occidentale* this portion of the tooth is relatively much narrower and the cusp is single. Associated with difference of structure is a marked difference in size between the species; *C. dakotensis* is larger and more robust in every way. This is made more apparent by a comparison of the following measurements:

<table>
<thead>
<tr>
<th></th>
<th><em>C. dakotensis</em></th>
<th><em>C. occidentalis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of last two lower molars</td>
<td>.045</td>
<td>.034</td>
</tr>
<tr>
<td>Length of last lower molar</td>
<td>.025</td>
<td>.019</td>
</tr>
<tr>
<td>Length of last two lower premolars</td>
<td>.027</td>
<td>.021</td>
</tr>
<tr>
<td>Width of crown of last lower premolar</td>
<td>.010</td>
<td>.013</td>
</tr>
<tr>
<td>Total length of upper molar series</td>
<td>.091</td>
<td>—</td>
</tr>
<tr>
<td>Length of premolars above</td>
<td>.041</td>
<td>—</td>
</tr>
</tbody>
</table>

This species is from the Metamynodon layer, and was found by Mr. O. A. Peterson, a member of the party.

**Colodon procuspidatus**, sp. nov.

This species is proposed upon a complete superior maxillary dentition of the right side, in which the last molar is wanting (No. 1215). So far as the measurements are concerned, it agrees very closely in size with *C. dakotensis*. The most important difference between this species and *C. dakotensis* is seen in the

\[\text{Loc. cit., p. 175.}\]
degree of separation of the internal cusps of the premolars from each other, and the more decided approach towards the structure of the molars. In the second premolar the two internal cusps are almost as distinct as they are in the molars; in the third premolar they are less so, while in the fourth they are separated by scarcely more than a vertical groove on the internal face of the crown. The cross-crests are more prominent than in the premolars of *C. dakotensis*, but the two external cusps are apparently not so distinct from each other as in that species. The external and internal cingula are prominent and distinct. The only means at present known of distinguishing *C. procuspidatus* from *C. occidentale* is by the smaller size and generally less robust character of the latter.

Found in the Metamynodon layer by Mr. J. W. Gidley.

**Lower Milk Molars of *C. occidentalis***.—The inferior milk molar dentition of this species is represented in our collections by two fragmentary lower jaws (Nos. 1044 and 1044a). With the exception of the first milk molar, which agrees very closely in size and structure with its corresponding premolar, the remaining two teeth of this series are of a more advanced pattern. They resemble the true molars in that the posterior cross-crest is complete and quite as well developed as the anterior. In the perma-
nent premolars the posterior crest is never complete, the heel of the tooth preserving its primitive arrangement of a separate external and internal cusp.

The total length of this series slightly exceeds that of the corresponding premolars.

**Colodon (?) longipes O. & W.**

**Syn. Mesohippus longipes O. & W.**

It seems proper in this connection to again call attention to the specimen which we have described under this name. It is probable that it is the foot of a species related to *Colodon*, although it differs in some important particulars from the fragmentary materials which we already know of *Colodon occidentale*. In some respects it resembles the Horses, but at the same time it presents such striking differences from any known members of this series as to absolutely prohibit its reference to any of the Equidae. These differences may be summarized as follows: (1) The continuity of the ectal and sustentacular facets of the astragalus, as in the Rhinoceroses and Hyracodons generally; (2) the great vertical depth of the ectocuneiform; and (3) the articulation of metacarpal IV with the ectocuneiform, thus excluding the contact between the cuboid and metacarpal III, an extremely constant and highly diagnostic feature of all the Horses.

Its nearest prototype is apparently found in the foot of *Heptodon calciculus* of the Wahsatch. The two astragali are very similar in their details of structure, and the whole foot is strikingly similar in the two forms. Unfortunately the ectocuneiform is not preserved in our specimen of *H. calciculus*. A comparison of the foot of *C. longipes* with that of *Triplopus amarorum* Cope, reveals the closest similarity in all details of structure. There can be very little doubt therefore that *C. longipes* is the direct successor of some species of *Helaletes* or *Triplopus*; and whether the foot in question is to be associated with any of the known species of *Colodon* is still an open question. We have therefore retained the specific name, and have provisionally referred it to the genus *Colodon*.

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Family HYRACODONTIDÆ.

We insert here a description of the skull of *Hyrachyus* from the Bridger Eocene, which is important in its bearing upon the relation of the primitive Hyracodons to the true Aceratheres or Rhinoceroses.

*Hyrachyus agrarius* Leidy.

The skull of this important species has been known hitherto only from specimens showing the upper and lower teeth, the jaws and the posterior portion of the occiput in the Leidy (Philadelphia Academy) and Cope collections. The American Museum collection from the Bridger includes many parts of the skeleton and a nearly perfect skull and jaws (No. 1645), as represented in Figs. 9, 10 and 11. It was figured upon a very small scale on Plate II of our earlier paper.

**Dentition.**—All the teeth are preserved excepting the upper incisors. The formula is typical, 3, 1, 4, 3. The incisors are compactly placed, and decrease in size from the median to the outer pair. The median lower incisors (i₁) are decidedly chisel-shaped or spatulate and nearly procumbent; the outer incisors (i₃) are the smallest of the series, as well as the most erect and pointed. The upper canine is slightly larger than the lower; both canines are vertically placed, laterally compressed and somewhat incisiform, rather than of the typical canine form; in fact they resemble a much enlarged lateral incisor. This is an important character.

**Upper Premolars.**—The premolars in both jaws are simpler than the molars, or pm. < m. The first is a small, laterally compressed tooth, with an internal cingulum. The second, third and fourth premolars (p₂₄) increase in complication, and present three successive stages of evolution toward the molar pattern; they are all triangular, and exhibit a backwardly hooked protoloph and thread-like posterior crest or rudimentary metaloph; there is also a trace of an incipient reduplication of the protocone in p₄₄, as shown in the accompanying sketches. This regular progressive evolution of the premolars from behind forwards is an impor-
tant distinctive character, for it is not what we find either in the Aceratheres or in the true Lophiodontidae, as here described. In the Aceratheres the anterior premolars acquire their transverse crests earlier than the posterior premolars.

In the Aceratheres the anterior premolars acquire their transverse crests earlier than the posterior premolars.

**Lower Premolars.**—These teeth exhibit a similar progression, the last being decidedly the most complex; they show a high, obliquely placed metalophid and a low, basin-shaped talonid, which exhibits no trace of the hypolophid or posterior crest.

**Molars.**—The molars are incipiently but not fully rhinocerotine, because the elongation of the paracone, and consequent asymmetry of the external cusps, which is the distinctive feature of the rhinoceros molar, has not progressed very far. The second molar is the largest and most progressive tooth of the series; it displays a prominent parastyle, traces of a cingulum at the base of the metacone, a prominent anterior cingulum, a feeble posterior cingulum, and an incomplete internal cingulum. It exhibits a strong protoloph, a more slender metalophid and a delicate crista, but there is no trace of an anticrochet or of a
crochet. The convexity of the paracone is still marked upon the outer surface of the ectoloph.

Skull.—The skull is delicately proportioned, and the cranium is surmounted by a prominent but thin crest. The total length is 12 inches (30.5 cm.); the greatest breadth across the zygomatic arches is 5½ inches (14 cm.). It is thus narrower in proportion to its length than the skull of *Colonoceras agrestis*, as figured by Marsh.¹ The deep facial region is in contrast with the small and rather slender cranial region, as in the skull of the ruminant Artiodactyla. As seen from above, the face appears twice as long as the cranium, if we take the divergence of the sagittal crests as the dividing point. But, taking the center of the orbits as the middle point, we find that the face and cranium are exactly equal in length. The extent of the frontals, parietals, occipitals and squamosals is exhibited in Fig. XI.

In superior view, the skull exhibits long nasals tapering to slender points and diverging anteriorly; a broad, slightly arched surface between the orbits; a long, thin sagittal crest diverging into low sagittal ridges; thin and delicate zygomatic arches; a small, rounded brain-case, and a very narrow supra-occipital region. In lateral view (Fig. XI) we observe that the premaxillaries extend upon the sides of the nasals; the extent of the lachrymals cannot be determined; the skull also exhibits a deep, lateral notch upon the anterior border of the nasals, which is also very characteristic of the lower Miocene Rhinoceros (*Aceratherium*); an infraorbital foramen above the third premolar; a large open orbit; a wide space between the post-glenoid and post-tympanic processes; the cranium pierced by numerous nutrient foramina; the occiput slightly overhanging the condyles; a long, delicate paroccipital process (partly broken off in this specimen) which is distinct or separated inferiorly from the postglenoid process. It is difficult to determine whether the mastoid portion of the periotic is exposed or not. The palate is somewhat injured, but the inferior view (Fig. XI) of the skull shows a considerable diastema between the canine and first premolar; a prominence of the cranial axis at the junction of the basi-occipital and basi-sphenoid; elongate or laterally compressed periotic masses opposite the

¹ *Dinocerata,* p. 64, Fig. 70.
entrance of the external auditory meatus. The occiput is laterally compressed; it narrows superiorly and slightly overhangs the condyles.

Foramina.—The alisphenoid canal pierces the sphenoid at the base of the pterygoids. The foramen ovale is peculiar in being very far back; it lies upon the outer side, slightly in front of the for. lac. medium. The for. lac. posterius is small. The post-glenoid foramen, the mastoid foramen, and the condylar foramen are well marked.
Measurements.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>M.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tip of nasals to summit of occipital crest</td>
<td>.305</td>
</tr>
<tr>
<td>Width of zygoma</td>
<td>.140</td>
</tr>
<tr>
<td>Height of occiput</td>
<td>.073</td>
</tr>
<tr>
<td>Length of molar-premolar series</td>
<td>.112</td>
</tr>
<tr>
<td>Length of lower jaw, angle to tips of incisors</td>
<td>.270</td>
</tr>
</tbody>
</table>

Lower Jaws.—The jaws are 10½ (27 cm.) inches in length. They exhibit a very slightly convex condyle; a narrow, strongly recurved coronoid process; a very deep, backwardly projecting angle with a sharply defined external and internal border. The rami taper anteriorly towards the shallow chin. The symphysis is 6.3 cm. in length and decidedly narrow.

This skull certainly bears a very close resemblance in many details to that of *A. mite*, and suggests at once that it stands in ancestral relationship to this true Aceratherium, but the skeletal characters of the two animals have been shown to be widely different. The differences in dentition are also marked: (1) *Hyrachyus* shows no traces of the unequal development of the incisors and canines which we may confidently anticipate in the direct ancestors of the Aceratheres at this period. (2) The premolar evolution follows a different law from that seen in the Aceratheres. (3) The molars exhibit a precocious development of the ‘crista’ (Fig. 12), a feature acquired slowly in the Aceratheres.

The strong resemblance between the *Hyrachyus agrarius* and *Aceratherium mite* skulls therefore is chiefly important, because it demonstrates almost conclusively that the Hyracodonts and Aceratheres were derived from a common stem form.

Family RHINOCEROTIDÆ.

Subfamily ACERATHERIINÆ.

Our list¹ of Aceratheres, published in July, 1894, requires revision. The specimens typical of *A. mite* Cope, from Colorado, exhibit a complete posterior crest in the fourth premolar, and are thus more progressive than the three skulls we referred to *A. mite*. In other respects the animals are closely similar. The *A. pumilum* Cope, from the Canada exposures, is as yet very imperfectly

Figure 22. *Asterina affinis.* A. Lower O同一m Beds. B, No. 1175, Upper O同一m Beds. C, No. 1199, Middle O同一m Beds. D, No. 1144, Lower O同一m Beds.
characterized. The *Diceratherium proavitus* of Hatcher proves to be identical with our *A. tridactylum*.

As regards geological distribution, it now appears certain that the predominant species of the Oreodon Beds was *A. occidentale* Leidy, although the *A. mite* occurs in the lower portion of these beds, and other species will undoubtedly be found in them. Leidy's type specimen, now in the National Museum, is characterized by a very simple condition of the fourth upper premolar, and was probably found upon the Lower Oreodon level; the grounds for this opinion are, (1) that No. 1107 in our collection, showing an identical stage of premolar development, was found in the lower Oreodon level; (2) that all the specimens from the Middle and Upper Oreodon Beds show a more progressive condition of the fourth premolar than Leidy's type; also a larger size of skull.

As regards specific succession, it is now certain that *A. occidentale* was directly ancestral to *A. tridactylum*, and it appears possible that *A. trigonodum* gave rise to *A. platycepalum*; in both, the horizontal or procumbent lower teeth is a marked characteristic. Much remains to be done upon the skeleton, and especially the feet, before the phyletic relationship of these species can be ascertained.

The large number of skulls in the collection belonging to *A. tridactylum* demonstrates that the species ran to two extremes, a high, long, narrow type, and a shorter, lower and broader type. The latter exhibit very prominent rugosities upon the nasals, which we might, with Hatcher, interpret as prophetic of *Dicera-

These two varieties of *A. tridactylum* are not due to age, but may be partly sexual. The molar structure shows no constant differences.

Family AMYNODONTIDÆ *S. & O.*

Genus **Metamynodon** *S. & O.*

**Matamynodon planifrons** *S. & O.*

PLATES X AND XI.

The Expedition of 1892 secured the skull and jaws of one animal (No. 555), and jaws of exactly the same size with the

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1 American Geologist, May, 1894, p. 360.
greater part of a skeleton of another animal (No. 546): namely, the vertebrae as far back as the 10th dorsal; many ribs of both sides, including an unbroken series, R. 1-14, on the right side; the left fore and right hind limbs complete. A vigorous search in 1894 supplemented these parts by a complete left hind foot (No. 1100), and an almost complete right fore foot (No. 1095). A complete left scapula (No. 1092) was also found with a pelvis belonging to an animal of slightly smaller size. These exceptional materials were supplemented by a few ribs, phalanges and caudals from other individuals. The spine of the axis is restored from another perfect specimen. The only parts of the skeleton which are entirely conjectural are the spines of the last cervical, and of four anterior dorsal vertebrae; also the entire lumbar series.

The animal has been mounted with great care and skill by Mr. Adam Hermann, as represented in the camera perspective drawings (Plates X and XI).

The following are the chief dimensions:

**Dimensions of Skeleton.**

<table>
<thead>
<tr>
<th></th>
<th>Feet</th>
<th>Inches</th>
<th>Metres</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length, tips of premaxillaries to bend of tail</td>
<td>9</td>
<td>7</td>
<td>2.93</td>
</tr>
<tr>
<td>Height</td>
<td>4</td>
<td>3(\frac{1}{2})</td>
<td>1.30</td>
</tr>
<tr>
<td>Breadth, across pelvis (Skeleton No. 1092)</td>
<td>2</td>
<td>3(\frac{1}{4})</td>
<td>.70</td>
</tr>
<tr>
<td>Hind limb, total length</td>
<td>3</td>
<td>4(\frac{1}{2})</td>
<td>1.03</td>
</tr>
<tr>
<td>Right innominate bone</td>
<td>1</td>
<td>9(\frac{1}{2})</td>
<td>.55</td>
</tr>
<tr>
<td>Femur</td>
<td>1</td>
<td>8</td>
<td>.50</td>
</tr>
<tr>
<td>Tibia</td>
<td>10</td>
<td></td>
<td>.27</td>
</tr>
<tr>
<td>Metatarsal III, length</td>
<td>4(\frac{3}{4})</td>
<td></td>
<td>1.15</td>
</tr>
<tr>
<td>Fore limb, total length, excluding scapula</td>
<td>3</td>
<td>5(\frac{1}{2})</td>
<td>1.05</td>
</tr>
<tr>
<td>Scapula</td>
<td>1</td>
<td>2</td>
<td>.35</td>
</tr>
<tr>
<td>Humerus</td>
<td>1</td>
<td>5(\frac{1}{2})</td>
<td>.43</td>
</tr>
<tr>
<td>Radius</td>
<td>1</td>
<td>1</td>
<td>.33</td>
</tr>
<tr>
<td>Ulna, including olecranon</td>
<td>1</td>
<td>5(\frac{1}{2})</td>
<td>.45</td>
</tr>
<tr>
<td>Metacarpal III, length</td>
<td>6</td>
<td>6(\frac{1}{4})</td>
<td>1.55</td>
</tr>
<tr>
<td>Skull length, premaxillaries to condyles</td>
<td>1</td>
<td>9(\frac{1}{4})</td>
<td>.55</td>
</tr>
<tr>
<td>Molar-premolar series</td>
<td>9</td>
<td></td>
<td>.23</td>
</tr>
<tr>
<td>Vertebral column, total length, including sacrals</td>
<td>6 10</td>
<td></td>
<td>2.09</td>
</tr>
<tr>
<td>7 Cervicals</td>
<td>1</td>
<td>9</td>
<td>.53</td>
</tr>
<tr>
<td>19 Dorsals</td>
<td>3</td>
<td>9(\frac{1}{2})</td>
<td>1.16</td>
</tr>
<tr>
<td>4 Lumbars</td>
<td>10(\frac{1}{4})</td>
<td></td>
<td>.26</td>
</tr>
<tr>
<td>Sacrals (estimated)</td>
<td>5(\frac{1}{4})</td>
<td></td>
<td>.135</td>
</tr>
<tr>
<td>Caudals</td>
<td>2</td>
<td>5(\frac{1}{2})</td>
<td>.735</td>
</tr>
<tr>
<td>Ribs, 1st Rib</td>
<td>1</td>
<td>2</td>
<td>.355</td>
</tr>
<tr>
<td>5th Rib</td>
<td>2</td>
<td>6</td>
<td>.76</td>
</tr>
<tr>
<td>9th Rib</td>
<td>2</td>
<td>8</td>
<td>.81</td>
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</tbody>
</table>
The animal in life was over nine feet long, about three feet broad through the chest, and nearly five feet high, for it is probable that the anterior dorsal spines were longer than here represented. The general impression is of a very large skull with formidable canine tusks, small but prominent eye-sockets, and very broad, flat skull. The fore and hind limbs are quite powerful, but the metapodials are rather slender, especially in the manus. The most distinctive feature of course is the four completely functional digits, which widely separate this animal from the true Rhinoceroses. The chest has a well-rounded barrel, and the lower border of the abdomen must have been quite low. The anterior ribs are flat, but from the R. 7 backwards they become rounded and rather slender.

The skeleton has already been described in some detail.1

VERTEBRAL COLUMN OF Titanotherium eobroni.
One-ninth natural size.
Pliosauridae

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BULLETIN
OF THE
American Museum of Natural History.

Volume I, 1881-86....................... Price, $4.25
" II, 1887-90...................... " 3.50
" III, 1890-91.................... " 3.00
" IV, 1892.................... " 3.00
" V, 1893.................... " 3.00
" VI, 1894.................... " 3.00
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