

MEMOIRS
OF THE
American Museum of Natural
History.

VOLUME I, PART III.

The Extinct Rhinoceroses.

By HENRY FAIRFIELD OSBORN.

April 22, 1898.

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PLATES XIII_a TO XX.

PREFACE TO THE MEMOIR.

One of the distinguishing features of a palæontological memoir is that it is of necessity incomplete. Even after long delay for the final collection of material the author is compelled to issue it while perfectly aware that fresh discoveries may be made at any moment which may controvert some of his chief conclusions.

This Memoir is at present planned to consist of seven parts, two of which are published herewith. Part I is mainly devoted to the morphology of the skull and teeth. Part II is based upon a very large and perfect series of skulls, many of them associated with more or less complete skeletons, from the White River Beds of Nebraska and Dakota. These were brought together by members of the American Museum Expeditions of 1892 and 1894, under the skillful leadership of Dr. J. L. Wortman. The skulls have been prepared and mounted under the direction of Mr. Hermann, Preparator, and systematically catalogued by Dr. W. D. Matthew.

The writer is greatly indebted to Prof. J. A. Allen, editor of the American Museum publications, as well as to Dr. W. D. Matthew, for careful revision of the proofs.

A more logical and satisfactory arrangement than that here adopted would have been to treat the entire structure of each species at once, but the delay in the collection and preparation of the skeletal material necessitated an introduction with the cranial and dental characters only. Again it would have been more satisfactory to have treated all the American Aceratheres together, but the Lower Miocene or John Day Rhinoceroses are still very imperfectly known or represented. As at present planned this Memoir will be continued as follows :

Part III.—Aceratheres of the American Miocene. Cranial and Dental Characters.

Part IV.—Aceratheres and Rhinoceroses of Europe in comparison with those of America.

Part V.—Skeletal Characters of American Aceratheres, and final classification of the Rhinocerotidæ.

Part VI.—The Arynodontidæ.

Part VII.—The Hyracodontidæ.

When complete, therefore, the Memoir will cover the superfamily Rhinocerotoidæ, or the extinct Rhinoceroses in the broadest sense as one of the grand divisions of the Perissodactyla. This is a portion of the author's studies upon the *Fossil Mammals of North America*, in coöperation with Professor W. B. Scott. No attempt has been made here at an exhaustive treatment of the literature or of the history of opinion.

The lesser problems of specific and generic definition, still unsettled, are insignificant when compared with the grand problems of the centre of origin of this group, of the relations between the Old World and New World forms, and of the succession and extinction of certain types. Both small and large problems depend alike upon correct methods of analysis and a philosophical estimate of the importance to be attached to characters of different kinds.

With strict regard to priority in the use of terms, especially in the generic and higher divisions, nomenclature should be treated as the tool or servant of our thought. It must express our conceptions, and be sufficiently

plastic to conform to the progress of our discoveries. Unfortunately, by too many writers, this normal and reasonable relation is reversed, and thought is made the servant of nomenclature. If we divide the RHINOCEROTOIDEA into three families, *Rhinocerotidæ*, *Amynodontidæ* and *Hyracodontidæ*, we clearly express our conception of three great phyla, related only in their origin. If we divide the *Rhinocerotidæ* into four subfamilies, we clearly express the conception of one primitive and three specialized and finally independent branches or sub-phyla. Thus the superfamily, family and sub-family terms all serve their purpose. In treating of the taxonomy of the Horses, the steps in each of such sub-phyla we may designate as genera, but in the taxonomy of Rhinoceroses it may subserve the clearness of our thought better to designate these steps as species.

Throughout, one single purpose has been kept in view, namely, to establish *a sound philosophical basis for the morphology of the Rhinoceroses, derived from their primitive, parallel and divergent characters, and leading toward the discovery of their origin, phylogeny and distribution.*

H. F. O.

AMERICAN MUSEUM OF NATURAL HISTORY,

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Part I.—MORPHOLOGY OF THE SKULL AND TEETH.

I.—Introduction. Differentiation of the Hyracodonts, Amynodonts and true Rhinoceroses.

The *Perissodactyla* may be primarily divided¹ by the fundamental pattern of their upper grinding teeth into four superfamilies, as follows :

- I. TITANOTHERIOIDEA : including the single family 1. *Titanotheriidae*.
- II. HIPPOIDEA : including the two families 2. *Equidae* and 3. *Palæotheriidae*.
- III. TAPIROIDEA : including the two families 4. *Tapiridae* and 5. *Lophiodontidae*.
- IV. RHINOCEROTOIDEA : including the three families 6. *Hyracodontidae*, 7. *Amynodontidae* and 8. *Rhinocerotidae*.

To these should probably be added V. CHALICOTHERIOIDEA, an aberrant superfamily, with molar teeth related to the Titanotheres pattern, and perissodactyl feet provided secondarily with claws.

The eight families, in the order named, may be imagined as contemporary branches of the four superfamilies ; these in turn having branches from a still unknown Perissodactyl stem form—probably a Cretaceous member of the Condylarthra.

These eight families, familiarly known as the Titanotheres, Horses, Palæotheres, Tapirs, Lophiodonts, Hyracodonts, Amynodonts and Rhinoceroses, when regarded as a series, present upon the one side close resemblances, or perhaps affinities, to the Artiodactyla, and an extreme departure from the Artiodactyla upon the other. Thus the Titanotheres exhibit many resemblances to the Artiodactyls, while the Rhinoceroses exhibit none at all, and are in many respects the most typical Perissodactyls.

¹ Compare Schlosser (1886); Osborn (1892, p. 90; also 1893, p. 36).

Superfamily IV. RHINOCEROTOIDEA,

OR

RHINOCEROTINE GROUP.

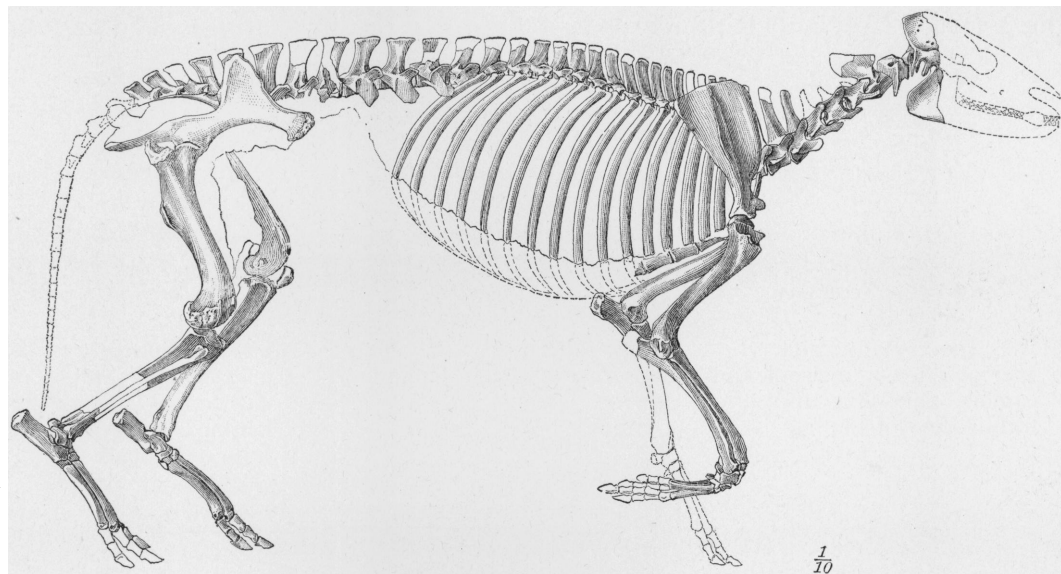
The three distinct families included in this division may be popularly known as the Cursorial or Upland Rhinoceroses, the Aquatic Rhinoceroses and the True or Lowland Rhinoceroses. They are briefly distinguished as follows :

6. <i>Hyracodontidæ</i> .	7. <i>Amynodontidæ</i> .	8. <i>Rhinocerotidæ</i> .
CURSORIAL RHINOCEROSSES.	AQUATIC RHINOCEROSSES.	TRUE RHINOCEROSSES.
<i>Hyrachyus-Hyracodon</i> .	<i>Amynodon-Cadurcotherium</i> .	<i>Aceratherium-Rhinoceros</i> .
Manus functionally tridactyl. Upper and lower incisors and canines persistent and uni- formly developed.	Manus functionally tetradactyl. Incisors atrophied. Upper and lower canines greatly en- larged.	Manus functionally tridactyl. Upper canines atrophied. Me- dian upper incisors and lower canines opposed and irregu- larly developed.

Our knowledge of the three divisions of this superfamily extends back only to the Middle Eocene of America and Europe, namely, to the Bridger and the somewhat older Egerkingen Beds of Switzerland. No Rhinoceroses of any kind have as yet been found contemporary with the primitive Horses and Tapirs of the Wasatch of America, or Suessonian of France, but they will undoubtedly be discovered in these or older rocks, either in America or Europe, with characteristics as sharply defined as those of the other perissodactyl families.

Certainly before the Middle Eocene of North America, the RHINOCEROTOIDEA had here or in some unknown region specialized and diverged into the three above-mentioned families, which some authors place in the single family Rhinocerotidæ. While it is quite possible that in the Wasatch or Suessonian period this group consisted of a single family, in the Bridger we certainly find two distinct families, the Hyracodontidæ and Amynodontidæ, and in the White River these coexist with the Aceratheriinae, or ancestral true Rhinoceroses. The members of each family were evidently as widely different in their external form as in their dental and skeletal structure. The Hyracodonts and Amynodonts may be termed para-rhinoceroses, somewhat resembling the Rhinoceroses at the outset, but possessing different habits and developmental tendencies

which caused them to diverge very rapidly. Thus Cope separated the Hyracodontidæ in 1873 when he found that, unlike the true Rhinoceroses, all the upper and lower incisors were persistent. Osborn separated the Amynodontidæ in 1883 when the skull of *Amynodon antiquus* was discovered and found to differ from that of the true Rhinoceros in the development of large upper and lower canine tusks, and in the degeneration of the incisors. Every subsequent discovery has tended to widen rather than close the gaps between these side lines, which became extinct in the Oligocene, and the main line,



EOCENE HYRACODONT.

Figure 1. Skeleton of *Hyrachyus (eximius) agrarius*, as originally mounted. Collection of the American Museum of Natural History. After Cope, 'Tertiary Vertebrata,' 1883, Plate LIV.

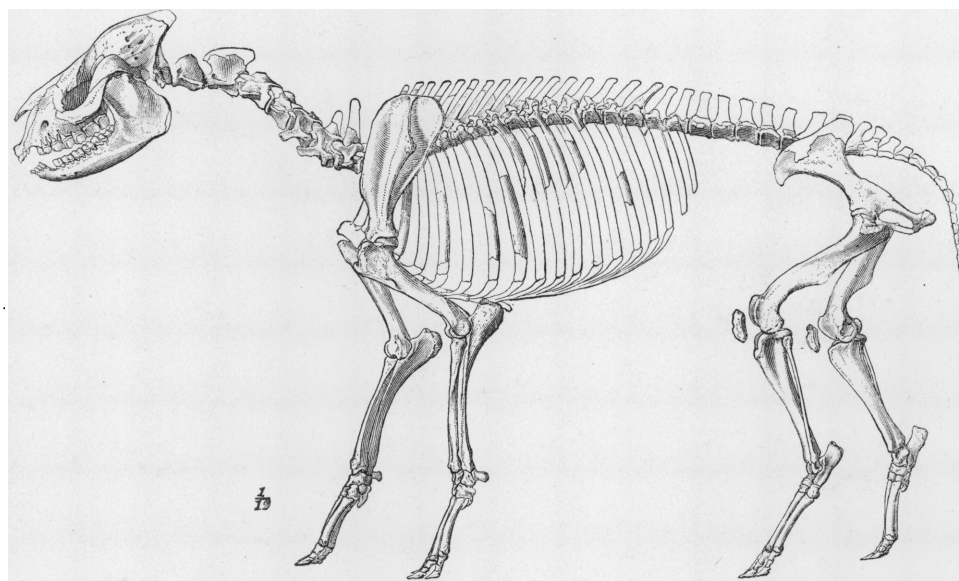
which persisted to the end of the Miocene in North America. Within the true Rhinocerotidæ we include four subfamilies, which also apparently represent several parallel and successive lines within the family proper, such as we observe in the Equidæ; these subfamilies are equivalent in part to the 'Groups' of Flower and Lydekker.

There is no doubt, therefore, that as a matter of taxonomic clearness as well as of phylogenetic fact it is best to consider these three families as entirely separate and undergoing a parallel development probably in Europe as well as in America.

Specialization in Habits.—The wide separation of these three families will be fully apparent after we have examined their chief primitive, parallel and divergent features. Parallelism is mainly confined to the evolution of the molar

teeth, for in every feature of the incisor teeth, the skull, the vertebræ and limbs, these families specialized and diverged rapidly. The rhinocerotine differentiation, in the broad sense of the term, imitated that of the Perissodactyla as a whole in its general functional radiation. They ran either into upland cursorial types, which competed with the Horses and Ruminants, or into lowland marsh or river dwellers, which competed with the Tapirs and Titanotheres.

Among the former were the smaller, more agile, light-chested types of Hyracodonts, simulating the Miocene Horses in skeletal structure and in the



OLIGOCENE HYRACODONT.

Figure 2. Restoration of *Hyracodon nebrascensis* Leidy, from materials in the E. M. Museum of Geology, Princeton University. After W. B. Scott (1895, Taf. III).

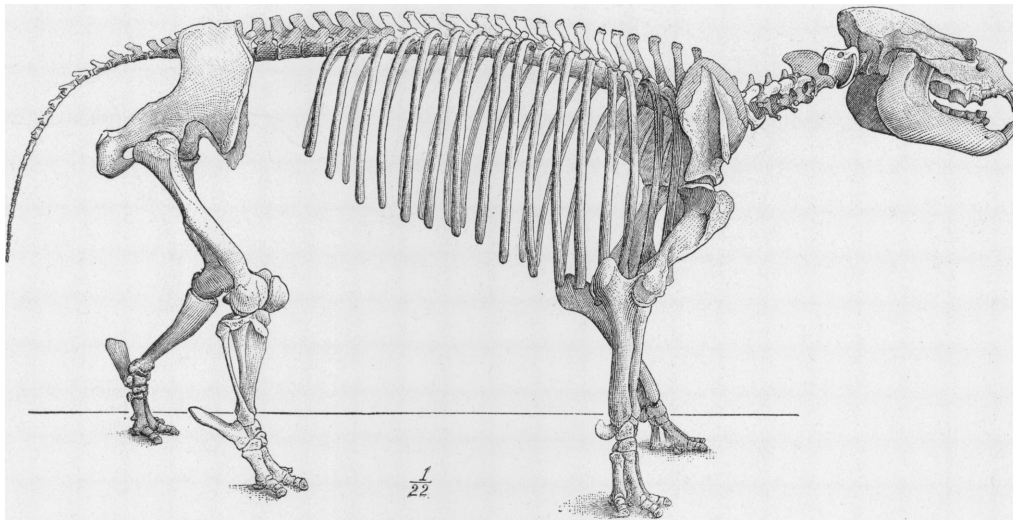
development of true hoofs.¹ Among the latter were the short, heavy types of Aynodonts, with broad, spreading, padded feet; they probably acquired, like the Tapirs, a long, prehensile upper lip, or, possibly, a true proboscis was developed, in correlation with the rather abbreviated nasals. The elevated and prominent position of the orbit would bring the eye near the surface in swimming. This feature, with the long, curved tusks, undoubtedly used in uprooting, suggests the resemblance between the habits of these animals and those of the Hippopotami. The early Aceratheres were light-limbed, rather swift-footed animals, intermediate in proportions between the Hyracodonts and Aynodonts, but far less graceful and rapid than the former; yet the destiny of this family was also to finally produce both the very slow, heavy-bodied

¹ Scott has recently (1896) made a very careful comparison between the Horse and Hyracodon skeletons.

forms, such as *Aceratherium* (*Aphelops*) *fossiger*, of the Loup Fork, and the stilted, long-limbed *Aceratherium malacorhinum* of the same period.

Neither the Hyracodonts or Amynodonts developed horns, and all the early true Rhinoceroses had weak, hornless nasals, so that they probably appeared externally more like enlarged modern Tapirs than the well-armed animals we are now familiar with.

They did not interfere with each other because each enjoyed a different local habitat while occupying the same general geographical regions. The

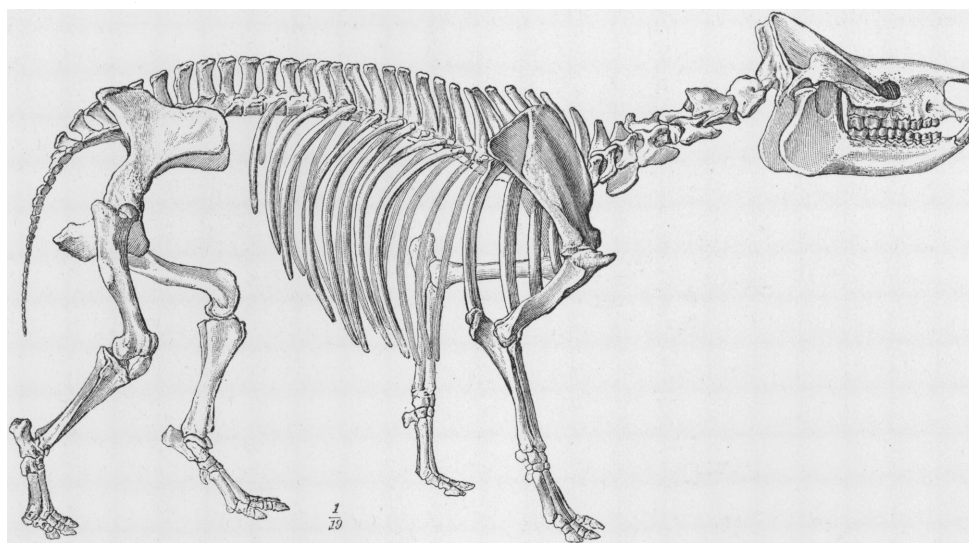


OLIGOCENE AMYNODONT.

Figure 3. Mounted Skeleton of *Metamynodon planifrons*. Collection of the American Museum of Natural History. After Osborn and Wortman (1895).

Hyracodonts dwelt in the drier grassy plains. The Amynodonts frequented the river and lake borders. Up to the time of the extinction of these two related families, the true Rhinoceroses maintained a somewhat uniform structure both in Europe and America, differing so far as we know in size rather than in proportions. Their dentition and their feeding habits were probably similar to those of the *R. bicornis* of Africa, and the *R. sondaicus* and *R. sumatrensis* of Asia, namely upon shrubs, leaves and softer herbage (see page 99). After the extinction of the rival families, however, there was naturally a tendency on the part of the true Rhinoceroses to enter the peculiar local habitats previously occupied by the Hyracodonts and Amynodonts, and they accordingly diverged into upland and lowland, short and long-limbed, brachydont and hypsodont types.

Geological and Geographical Distribution.—I. The Hyracodontidæ, including *Hyrachyus*, *Triplopus* and *Hyracodon*, are very abundant; displaying a great range of size in the Middle Eocene and Oligocene of North America, and are possibly represented in the Eocene of Europe by species which have been mistakenly referred by Rüttimeyer and others to *Lophiodon*. II. The Amaryndontidæ are known from the Upper Eocene or Washakie and Uinta Beds of North America, and are also possibly represented by species referred to *Lophiodon* in the Eocene of Europe, although it is difficult to determine this



OLIGOCENE ACERATHERE.

Figure 4. Mounted Skeleton of *Aceratherium tridactylum* Osborn, from the Protoceras Beds, Upper Oligocene of South Dakota. Collection of the American Museum of Natural History. After Osborn and Wortman (1894).

from the teeth alone; the latest American type is *Metamynodon* of the Oligocene, but *Cadurcotherium* represents a later and probably final stage of development in the Oligocene and Lower Miocene of France. III. The Rhinocerotidæ are first doubtfully known in the Upper Eocene of Europe, then suddenly appear in abundance in the Lower Oligocene. They are grouped in four subfamilies. 1. Aceratheriinae of Europe and America. These hornless types ranged through all the Miocene of North America, and then apparently became extinct upon this continent, but in Europe they extended into the Pliocene, and in Asia into the Middle Pliocene. 2. The Diceratheriinae, or pair-horned types, have been found only in the Lower and Middle Miocene of North America and Europe. 3. The earliest Rhinocerotinae, or Rhinoceroses possessing median horns, branched off from the Aceratheres in the

Middle Miocene of Europe; they divided into three subseries which are scattered widely over Europe, Asia and Africa, and displayed a remarkable specialization. 4. The most aberrant subfamily is the Elasmotheriinae, thus far found only in the Pleistocene of Siberia.

DISTRIBUTION TABLE, AMERICAN HORIZONS.

	Lower Eocene. <i>Wasatch.</i>	Middle Eocene. <i>Bridger.</i>	Upper Eocene. <i>Uinta.</i>	Oligocene. <i>White River.</i>	Lower Miocene. <i>John Day.</i>	Upper Miocene. <i>Loup Fork.</i>
I. HYRACODONTIDÆ						
<i>Hyrachyinae</i>						
<i>Hyrachyus</i>		×				
<i>Colonoceros</i>		×				
<i>Triplopodinae</i>						
<i>Triplopus</i>			×			
<i>Hyracodontinae</i>						
<i>Hyracodon</i>				×		
II. AMYNODONTIDÆ						
<i>Amynodon</i>		×				
<i>Metamynodon</i>				×		
<i>Cadurcotherium</i> ¹						
III. RHINOCEROTIDÆ						
<i>Aceratheriinae</i>				×	×	×
<i>Diceratheriinae</i>					×	
<i>Rhinocerotinae</i>						

I.—PRIMITIVE CRANIAL CHARACTERS.

The oldest rhinocerotine skeleton known is that of *Hyrachyus agrarius*, the Bridger Hyracodont, which is already so considerably modified that it cannot be considered an ancestor of either the Amynodons or Aceratheres, so we look further back for the actual stem type. It is quite possible, however, that the *Rhinocerotidæ* may have sprung from some less specialized member of the *Hyracodontidæ*.

From the primitive Perissodactyl was undoubtedly derived a stem *Rhinocerotoid type* which lived even earlier than the Bridger Period, perhaps as

¹ Phosphorites of Quercy.

early or earlier than the Wasatch or Suessonian. The comparative osteology of the oldest representatives of each family known, namely, *Hyrachyus agrarius*, *Amynodon antiquus* and *Aceratherium trigonodum*, indicates that there was such a common or stem form, and that it was extremely ancient. These three animals resemble each other strikingly in many characters, and we can derive from them at least a conception of the ancestral skull.¹

In many features, however, the beautiful skull of *Hyrachyus agrarius* (see Plate XIIa) preserved in the American Museum is generalized or primitive, and will serve to illustrate the following description, although it differs from the primitive type in some respects.

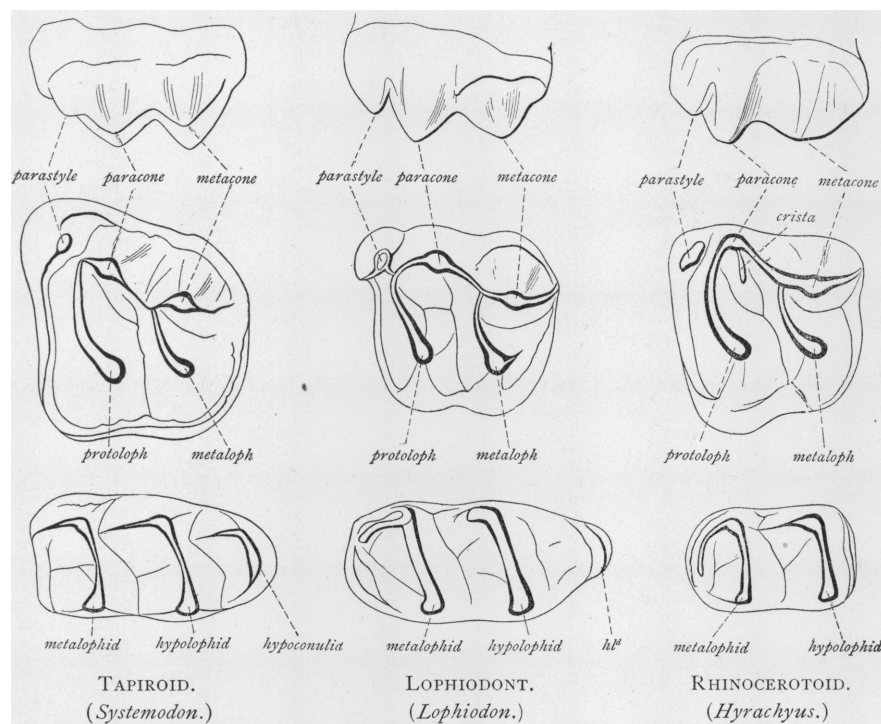
Skull.—The primitive skull was long and narrow, and the open orbit was placed above the second molar or half way between the condyles and tips of the premaxillaries. Thus the primitive facial region was relatively longer than in the modern Rhinoceroses. The nasals were smooth, narrow, overhanging the anterior nares, and articulating broadly with the premaxillaries. The cranium was surmounted by a thin, arching, sagittal crest which did not diverge anteriorly into supraorbital ridges. The occiput was relatively small and low, spreading slightly at the upper border and below. The occipital condyles were slender and projecting, and the post-glenoid process was extended transversely behind the glenoid cavity, there being no post-cotyloid process upon the slender posterior margin of the mandible. The region of the ear is very important: the external auditory meatus was widely open below; the post-tympanic portion of the squamosal had a short styliform process; between this element and the exoccipitals was probably a considerable exposure of the mastoid portion of the periotic bone (present in *Amynodon*, wanting in *Hyrachyus*) as in the *Equidae*, and the paroccipital itself extended laterally into a short process. This space behind the ear was therefore broad and triangular as compared with the narrow ridge seen in modern forms. The base of the skull was distinguished from that of some of the more recent types by the separation of all the basi-cranial foramina.

2.—PRIMITIVE DENTAL CHARACTERS.

The primitive formula included a full eutherian series of incisors, canines, molars and premolars. A narrow diastema separated the lower canine from the lateral incisor, and behind both canines was a considerable diastema, it being noteworthy that the first upper and lower premolars always adhered to the grinding or cheek series in the Rhinocerotidea, instead of approaching the canines as in the Hippoid and Tapiroid groups. This first upper premolar is

¹ Compare Scott (1883, pp. 12-14).

more persistent than in the Lophiodontidæ. The incisors were small, pointed, vertically placed and equal sized; the canines were considerably larger and also pointed directly upwards. 1. *The early acquisition of completely lophoid molars* was one of the most distinctively primitive features of the Rhinocerotidea. Sharply defined transverse crests appear in both upper and lower molars of the oldest known Rhinoceroses, and a very advanced lophoid ectoloph in the upper molars. (See Figure 5.) 2. *The upper molars early*



LOPHODONT MOLAR TYPES.

Figure 5. These diagrams illustrate the symmetrical convex paracone and metacone of the Tapiroids, passing in the Lophiodonts to the asymmetrical, convex paracone and concave elongated metacone of the Rhinoceroses.

acquired a striking resemblance to those of the Rhinoceros. This is especially apparent when the teeth are partly worn. This is not a mere superficial likeness, but a fundamental similarity in all the details of modification of the primitive sextitubercular bunodont molar. *a.* As Cope pointed out (1873, p. 228), the character separating the Rhinoceroses from all other lophodonts is the *asymmetry of the external cusps, the metacone being longer than the paracone.* *b.* They are further distinguished by the mode of union of the transverse crests with the ectoloph; the protoloph always appears to spring from between the closely conjoined parastyle and paracone; it really arises

from the apex of the paracone just as the metaloph arises from near the apex of the metacone. In the Tapirs, as seen in Fig. 5, these crests spring respectively from the anterior bases of the paracone and metacone. The origin of the crests in the Rhinoceroses is similar to that in the typical Lophiodontidæ which are thus transitional between the Tapirs and Rhinoceroses. *c*. In both

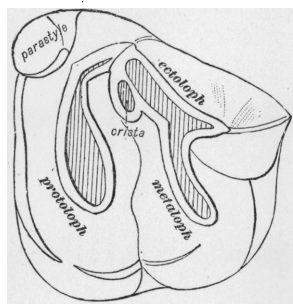
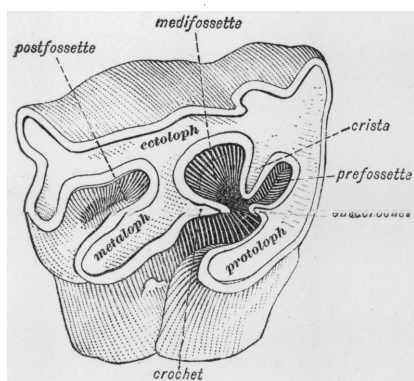


Figure 6. Superior Molar of *Hyrachyus agrarius*. Diagram representing the fundamental pattern.



TYPICAL RHINOCEROS MOLAR.

Figure 7. Rhinoceros Molar figured by De Blainville, *Ostéographie*, Plate XIII, Genus *Rhinoceros*. Species undetermined. Remarkable as presenting all the secondary folds and crests.

upper and lower molars the transverse crests are at oblique angles to the jaws; they slope strongly backwards upon the inner sides. This we have seen to be the primitive position of the perissodactyl crests, which was retained even in the latest members of this group. 3. A marked feature of the lower molars is the early loss of the third lobe; its absence distinguishes even the earlier Rhinoceroses from the Tapiridæ, Helaletidæ and Lophiodontidæ, all of which exhibit this lobe.

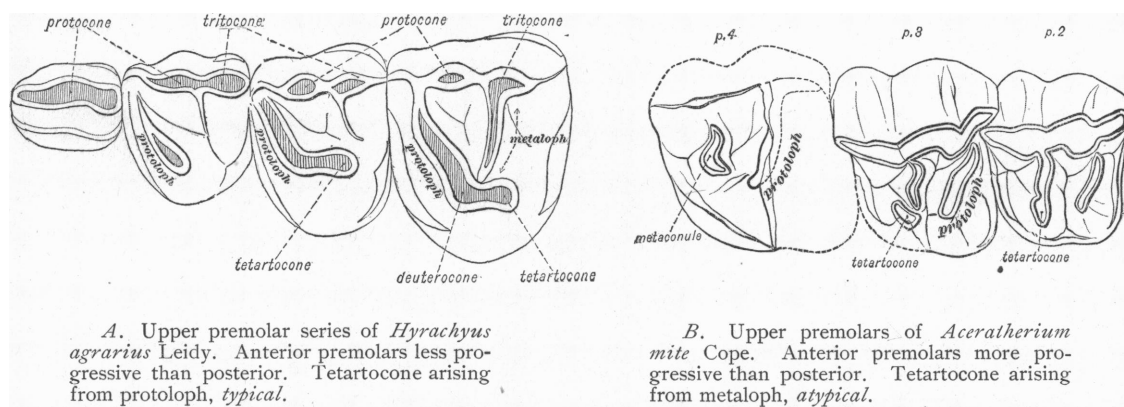
The upper cheek series of *Hyrachyus agrarius* also fill many of the conditions we expect to find in the ancestral molars of the Amynodonts and true Rhinoceroses; they represent a persistent early stage from which the other two families diverged more rapidly than the Hyracodonts. They are incipiently but not fully rhinocerotiform, because the elongation of the paracone, 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 recurved protoloph, a shorter metaloph and a delicate crista (Fig. 6).

3.—PARALLEL EVOLUTION OF THE MOLAR TEETH.

As shown in the comparative table upon page 80, there is absolute divergence in the development of the cutting teeth or incisors and canines in these three families. Parallelism is strictly confined to the cheek teeth.

1. Evidence of the primitive consanguinity of the members of this group is shown not only by the actual homologies of structure just described, but by the latent capacity for the independent development of many similar structures. To some such potentiality we attribute the *independent development of similar secondary crest folds* in the upper molars of widely separated generic lines. The 'antecrochet' and 'crista,' which spring from the proto-loph and ectoloph, are observed in all three families, appearing much earlier in some series than in others. The 'crochet,' or third fold, which springs from the metaloph, is peculiar to the true Rhinoceros molars, which are fully described on a later page. It is only feebly developed, if at all, in the Amynodonts and Hyracodonts.

Figure 8. PREMOLAR METAMORPHOSIS, DEVELOPMENT OF CRESTS.



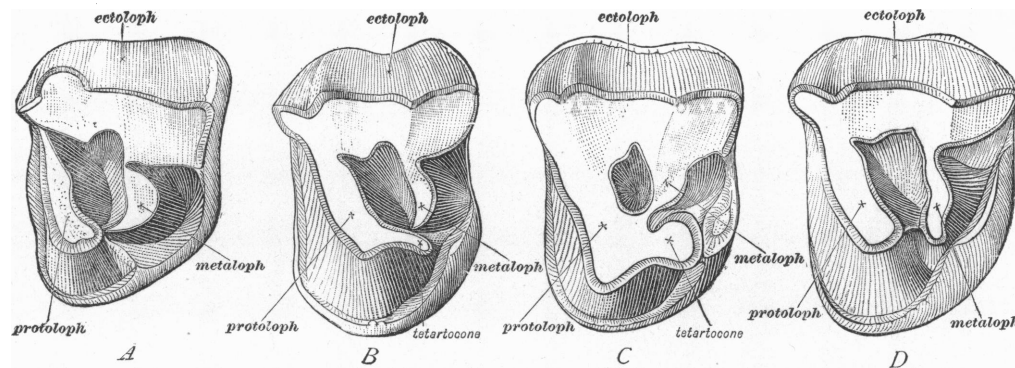
2. A second feature in which the Hyracodontidæ and many but not all of the Rhinocerotidæ progressed similarly was in the *mode of metamorphosis of the premolars* (Fig. 8).

We have found that in the Equidæ, Tapiridæ and in the Helaletinæ, the primitive single internal cusp or deuterocone of the posterior premolars early divides into two cusps, so that when the metaloph is developed it is from the first entirely separated from the protoloph; the latter is true also of the Amynodontidæ, and of certain atypical Aceratheres.

In the Hyracodonts and typical Aceratheres, on the contrary, the external portion of the metaloph is developed before the deuterocone of the protoloph gives off the tetartocone. This gives the protoloph a highly characteristic backward hook (Fig. 9), and explains why in the Hyracodonts and certain early Rhinoceroses, such as *A. copei* and *A. occidentale*, the proto- and metalophs of the premolars unite internally when the crown is partly worn down. The exception to this, or *atypical* development, is seen in certain species of

Aceratheres (*A. mite* and *A. trigonodum*), in which the tetartocone is budded off near the metaloph (Fig. 8a).

The typical premolar transformation is well illustrated in *Hyrachyus agrarius*. The second, third and fourth upper premolars (pm^{2-4}) present three successive stages of evolution towards the molar pattern; they are all triangular and exhibit a backwardly-hooked protoloph and thread-like or incipient metaloph; there is also a faint trace of an incipient reduplication of the deutocone in pm^4 , as shown in the accompanying figure. This regular



TYPICAL PREMOLAR METAMORPHOSIS.

Figure 9. Fourth superior premolars in four specimens of *Aceratherium occidentale*, taken from successive geological levels. Collection of the American Museum of Natural History. After Osborn and Wortman (1895).

progressive evolution, most rapid in the fourth premolar,¹ is an important feature. The *lower* premolars of *Hyrachyus* exhibit a similar progression, the last being decidedly the most complex; they show a high obliquely-placed metalophid (crest connecting the protoconid and metaconid), and a low basin-shaped talonid which exhibits no trace of the hypolophid (posterior transverse crest connecting hypoconid and entoconid).

3. The selenoid transformation of the lower molars in the three families is very similar, for they develop secondarily and simultaneously from the outer borders long incurved spurs, such as are seen in the Equidæ and Titanotheriidæ, but not in the Tapiridæ, so that the hypolophid unites with the metalophid, and the primitively simple crests become selenoid. This tendency is so universal that it is very difficult to distinguish the Rhinoceroses of the three families by the form of the lower molars.

¹ The *Aceratheres* present an exception to this, because the transformation is most rapid in the second premolar. That is, pm^2 first acquires the molar pattern, then pm^3 , then pm^4 . (See divergent characters.)

4.—DIVERGENT EVOLUTION OF THE SKULL.

The divergence of the Rhinoceros from the primitive type of Perissodactyl, as well as the divergence of the three Rhinoceros families from each other, was well marked by the Upper Eocene period, and is fully discussed in the following pages.

The skull was affected by various modifications of the primitive proportions, seen especially in (1) the relative development of the face and cranium; (2) in the greater or less recession of the nasals; (3) in the widening of the gap between the nasals and the premaxillaries; (4) in the relative reduction and separation of the premaxillaries. At the side of the skull (5) there was a varying tendency to close the external auditory meatus inferiorly by the union of the post-tympanic with the post-glenoid processes; (6) at the same time the post-tympanic united more closely with the paroccipital and tended to cover up the exposed portion of the mastoid. (7) In the base of the skull the foramina became more or less confluent; (8) there was a rapid increase in the size of the brain, and (9) a greater or less reduction of the sagittal crest. The final result of these divergent modifications of the skull, as they affected the three families, is presented in the Table upon page 92.

5.—DIVERGENT EVOLUTION OF THE TEETH.

As already noted in Section 3, in the teeth we observe wide divergencies which may be summarized as follows :

1. In the relative persistence or reduction, hypertrophy or atrophy, of the canines and incisors.

2. In the varying *degrees* to which the metamorphosis of the premolars into molar form was carried, and in the proportions of size between the molars and premolars.

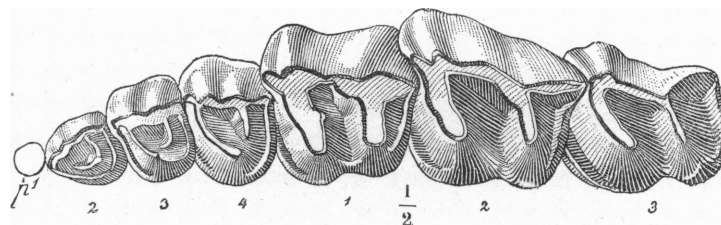


Figure 10. Premolar-molar series of *Metamynodon planifrons*, showing small size and arrested metamorphosis of premolars and of posterior valley in last upper molar caused by persistent ectoloph.

3. In the *methods* of cusp and crest addition by which the metamorphosis of the premolars was effected.

4. In the *order* in which the premolars metamorphose. In the Hyracodontidæ and Amynodontidæ (as in most Perissodactyla) pm^4 is the first to acquire the molar pattern, pm^2 being the last; in the Rhinocerotidæ, pm^4 is often the last to acquire the molar pattern, pm^2 being the first.
5. In the persistence or reduction of the ectoloph of the last upper molar. In the Amynodontidæ it persists; in the Hyracodontidæ, and in most of the Rhinocerotidæ, it is reduced.

SUMMARY OF EVOLUTION.

<i>Primitive.</i>	<i>Parallel.</i>	<i>Divergent.</i>
Skull elongate. Face and cranium equal. Orbits open. Nasals and premaxillaries in contact. Occiput low. Thin sagittal crest. Auditory meatus open. Mastoid exposed. Foramina distinct. Postglenoid process broad. Incisors and canines typical. Premolars unlike molars. Molars without folds. Lower molars ortholophoid. Manus tetradactyl. Pes tridactyl. Slight displacement.	Premolars metamorphosed. Molars with 'antecrochet' and 'crista.' Lower molars selolophoid.	Skull elevated. Cranium and face unequal. Sagittal crest thickened, reduced or obsolete. Premaxillaries reduced or separated from nasals. Auditory meatus open or closed below. Mastoid covered. Foramina confluent. Atrophy or hypertrophy of incisors, canines and premolars. Premolars and molars brachydont or hypsodont. Molars with 'crochet.' M^3 with ectoloph reduced, triangular. Manus tridactyl or tetradactyl. Extensive podial displacement.

6.—FINAL DIVERGENCE OF THE THREE FAMILIES.

The separation of the members of the rhinocerotine group illustrates beautifully the principle that *divergence arises not only from the mode but from the rate or relative rapidity of transformation*, for exactly similar structures are acquired in one family in the Eocene, in another in the Oligocene, in another in the Miocene, and so on. Thus the middle Eocene foot of the Hyracodontidæ is comparable to the lower Eocene foot of the European Rhinocerotidæ. The Amynodontidæ display in the Oligocene a degree of hypsodontism which was not acquired by any of the true Rhinocerotidæ until the Pleistocene; yet in the Amynodontidæ the rapid specialization of the teeth is accompanied by an absolutely stationary condition of the feet.

The Hyracodontidæ are broadly distinguished, in addition to the characters noted on page 88, by the persistence of primitive characters in the skull,

such as the complete typical upper series of incisors and canines, and the retention of the primitive proportions and relations of the bones of the skull. The premolars and molars develop into a nearly uniform cheek series resembling externally those of the Horses and remaining brachydont. The third superior molar has its ectoloph reduced and becomes triangular, as in most of the true Rhinoceroses. Tridactylism is rapidly acquired with a tendency to monodactylism in the lower Oligocene. The fifth digit of the fore foot is early reduced. The hind foot is extremely narrow; and as in the Horses, the astragalus does not extend upon the cuboid anteriorly. The skeleton is slender. The dorso-lumbar vertebræ are much more numerous, D. L. = 26, than in the Rhinoceroses.

The Amynodontidæ soon acquired a highly modified skull; the face is greatly shortened and the cranium elongated and flattened, with a strong, persistent sagittal crest. The maxillaries are deeply excavated in front of the orbits; the premaxillaries broaden, uniting with the nasals and with each other. The meatus auditorius becomes closed inferiorly and the mastoid

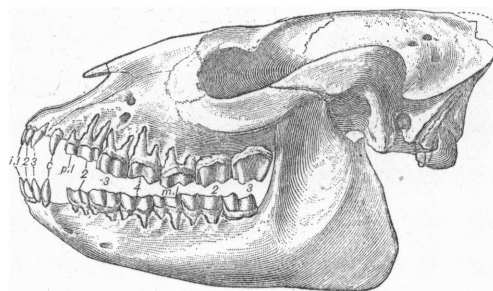


Figure 11. Skull of *Hyracodon nebrascense* Leidy, showing last stage of development in the typical Hyracodonts. Collection of the American Museum of Natural History.

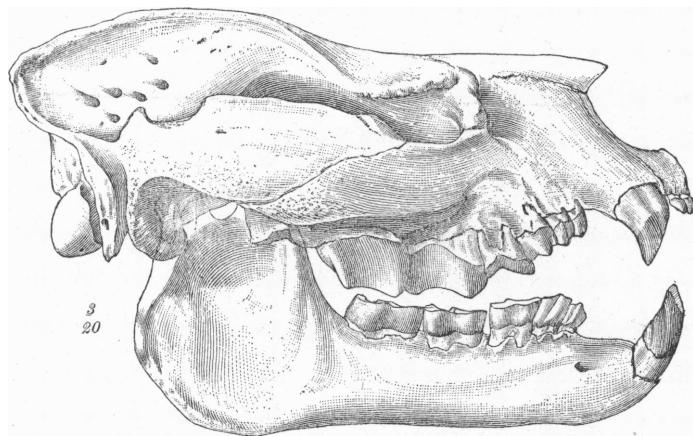


Figure 12. Skull of *Metamynodon planifrons*. Collection of the American Museum of Natural History.

covered. The complete upper and lower series of incisors are retained, but the canines develop into greatly enlarged, vertical tusks in both jaws. The premolars are reduced and the molars enlarged, finally becoming hypsodont (Oligocene). The third superior molar has a complete ectoloph, a posterior valley, and quadrate form, as in the Tapirs. The fore foot remains spreading and functionally tetradactyl.

In the Rhinocerotidæ the face is somewhat shortened, while the cranium is elongated and elevated. The premaxillaries are rapidly reduced and lose their sutural union with each other and with the nasals. The sagittal crest is replaced by a broad, flattened area. The whole incisor-canine series is

variable ; the upper canines early disappear, together with the lower median incisors. The premolars are fully metamorphosed, and pm^{2-4} remain large and functional. The third superior molar early becomes triangular by the loss of the posterior valley or union of the ectoloph with the metaloph; only a few types (*R. simus*, *R. antiquitatis*, *Elasmotherium*) are known in

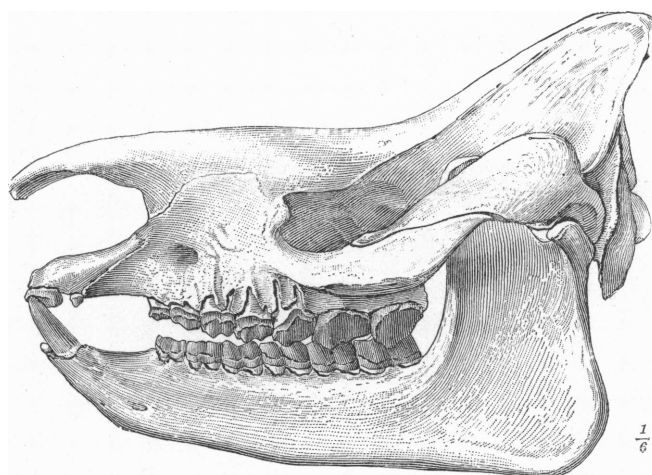


Figure 13. Skull of *Aceratherium tridactylum*. Type. Collection of the American Museum of Natural History.

which the complete ectoloph and posterior valley persist. Hypsodontism is very slowly acquired (Pliocene and Recent). Tridactylism is acquired in the lower Oligocene in some species (*A. mite*) and not until the summit of the Miocene in others (*A. tetradactylum*, *A. incisivum*), the fifth digit being long retained in the manus. The astragalus is widely displaced upon the cuboid.

SUMMARY OF FAMILY CHARACTERS.

<i>Hyracodontidæ.</i>	<i>Amyndodontidæ.</i>	<i>Rhinocerotidæ.</i>
Incisors normal. Canines atrophic, becoming incisiform. M^3 triangular, ectoloph in same line with metaloph, confluent. 'Crista' and 'antecrochet.' Post-glenoid process broad. No post-cotyloid process upon mandible. Face and cranium equal. Cranium heightened.	Incisors atrophic. Upper and lower canines hypertrophic. M^3 subquadrate; ectoloph at right angles to metaloph. 'Antecrochet,' no 'crista.' Post-glenoid process broad. No post-cotyloid process upon the mandible. Face shortened. Cranium broadened and flattened.	Incisors and upper canines atrophic. Lower canines enlarged, procumbent; or all cutting teeth atrophic. M^3 typically triangular; ectoloph in same line with metaloph. Post-glenoid process narrow. Large post-cotyloid process upon mandible. Face and cranium equal.

II.—THE TRUE RHINOCEROSSES.

FAMILY 8.—RHINOCEROTIDÆ.

Among the Perissodactyla the true Rhinoceroses rank next the Horses in interest to the evolutionist, for as early as the middle Miocene period they had passed the general stage of modification which the Tapirs exhibit at the present time ; in fact, it may be said that the modern Tapir gives us a very fair idea of the general size and structure of the true Oligocene Rhinoceros, not in the skull but in many characters of the vertebræ as well as in the form of the feet and limbs, and therefore probably in the mode of progression also.

The later members of the Rhinocerotidæ were closely united by many adaptive tendencies or potentialities of similar evolution which led to the same structural types being acquired over and over again. As regards the skull and dentition, the main centres of rapid evolution were the regions of the cutting teeth and of the nasals. The most distinctive feature was the universal loss of the upper canines, followed in many series by the loss of the incisors, so that the edentulous premaxillaries became weak and separate, as in certain Ruminants. As for the *nasals*, the old Roman name *Rhinoceros*, of Pliny, has been a misnomer ever since the Acerathine series was discovered by Kaup, for, in some series, notably those in India and North America, the nasals continued smooth and were rapidly reduced ; in the persistent European, Asiatic and African types they became elongated and bore horns, while in others again the nasals continued reduced and smooth, and the *frontals* developed a prodigious dermal horn (*Elasmotherium*).

The Rhinoceros skull and lower jaw underwent the most diverse modifications in correlation with the above determining factors of evolution.

According to the hornless or horned condition of the skull and the necessity of greater or less power behind it, the whole vertebral column was modified. The original molar type, as we have seen, is shared by the Hyracodonts and Amynodonts, but in the extreme development of the molars we find many analogies to the equine type, such as the foldings of enamel, the elongation of the crown and the deposition of cement. As a rule, the long slender feet of early types became short, heavy and spreading, the extremes being in *A. fossiger* of America, and *R. brachypus* and *R. aurelianensis* of

Europe. But in the Upper Miocene *A. malacorhinum* of America or Pleistocene *R. etruscus* of Europe, we find a persistence of the long, stilted metapodials of the early types.

1.—ANATOMY, FEEDING HABITS AND DISTRIBUTION OF THE LIVING RHINOCEROSES AS A KEY TO THE HABITS OF EXTINCT SPECIES.

As the problem of the origin of the living Rhinoceroses is still an unsolved and extremely interesting one, which will be discussed later in this Memoir, we derive especially from Flower (1876, 1891) the following account of the five extant species in relation to the brachydont and hypsodont forms of dentition and to their foot structure.

There are, first, the three *Asiatic* species, *with functional cutting teeth*, which may be arranged in order of specialization as follows :

A. The most primitive living Rhinoceros, *with two horns, a large nasal and small separate frontal, small partly functional cutting teeth* (I.†C.‡), *postglenoid and posttympanic processes separated*.

1. *R. sumatrensis* (*Ceratorhinus* of Gray) is of smaller size, combining primitive and specialized characters ; distinguished by its low, narrow occiput sloping backwards, external auditory meatus open below, reduced cutting teeth (the lateral upper and central lower incisors usually disappearing), molars short-crowned and otherwise similar to those of *R. sondaicus*. This species is closely related in its soft anatomy to the second Asiatic form, *R. sondaicus*.

B. Two species, *with one nasal horn, fully functional cutting teeth* (I.†C.‡), *and wide postglenoid-posttympanic union*.

2. The smaller, less modified *R. sondaicus*, or *javanicus*, is characterized by a low forwardly-sloping occiput and a smaller nasal horn, feeble or absent in the female (*R. inermis* Lesson); the comparatively short-crowned or brachydont molars are without cement, and exhibit a waving ectoloph with a strong buttress or parastyle, the transverse crests wearing into ridges, a large 'crochet,' but rarely a 'crista,' producing no 'fossettes' (see Fig. 14).

3. The large, highly-modified *R. unicornis* or *indicus* is characterized by a high forward-sloping occiput and a large nasal horn ; the high crowned (sub-hypsodont) molars exhibit a cement layer, a flattened ectoloph with obsolete parastyle fold, oblique protoloph and metaloph wearing horizontally, a large 'crochet' and 'crista' producing a 'medi-fossette' (see Fig. 14).

Second, there are the two *African* species (*Atelodus* of Pomel) :

C. With cutting teeth vestigial or wanting (I. & C. &), two horns placed close together, postglenoid and posttympanic partly separate, namely :

4. The *R. bicornis*, a smaller species which exhibits vestigial incisors in the young state only ; molars with short crowns and a delicate cement layer, protoloph and metaloph transverse, ectoloph with anterior buttress or parastyle fold, a large 'crochet' and a 'crista,' rarely uniting (molars of the same general type as in *R. sondaicus* and *R. sumatrensis*).

5. The *R. simus* is a large, highly modified species, with a broad, rather low occiput and no second cutting teeth, even in the young stage ; molars (like those of *R. unicornis*) sub-hypsodont, with a thick cement layer, flattened ectoloph without parastyle fold, protoloph and metaloph oblique, 'crochet' and 'crista,' generally united. This species is also distinguished from all recent and fossil Rhinoceroses (except *R. blanfordi* and *R. antiquitatis*) by the presence of a post-fossette in the third upper molar.

Glancing over the skulls, cutting teeth and molars of these three species, we see at once that there are many striking combinations of specialized with unspecialized characters, for there is no general specialization extending to all parts of the skeleton and teeth such as we observe in the Horses. The



Figure 14. SKULLS OF LIVING RHINOCEROSSES.
Rhinoceros sumatrensis. *Rhinoceros unicornis.*
Rhinoceros sondaicus. *Rhinoceros bicornis.*
Rhinoceros simus.

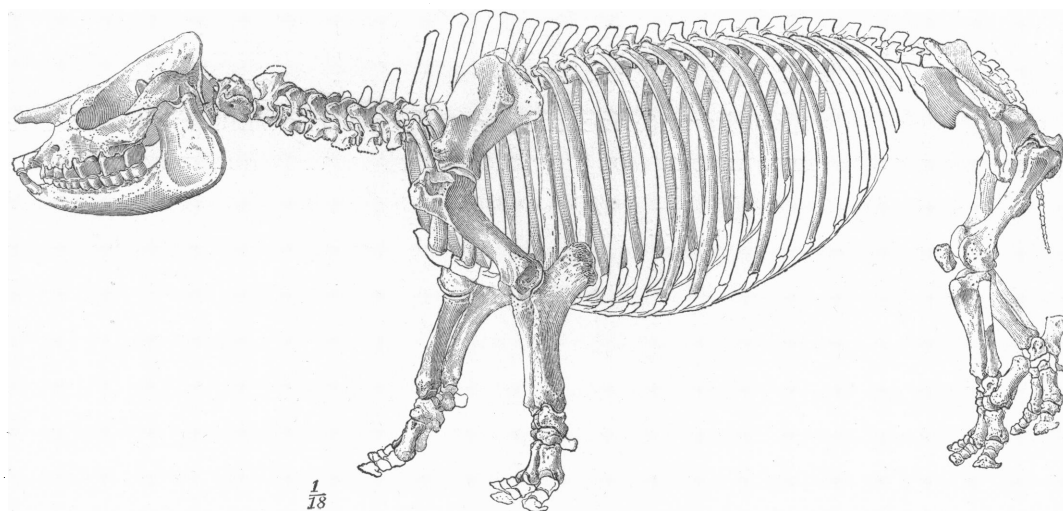
brachydont *R. bicornis* and hypsodont *R. simus* partly inhabit the same general regions of Africa, yet they exhibit entirely different feeding habits. But the former (*R. bicornis*) with its short-crowned molars has a prehensile upper lip and feeds exclusively upon the leaves and branches of bushes and small trees, and chiefly frequents woody and well-watered districts and the sides of wood-clad, rugged hills. Similarly the Javan and Sumatran Rhinoceroses (*R. sondaicus*, *R. sumatrensis*), with brachydont molars, have an insular and lowland range. In contrast, *R. simus*, of Africa, with its long-crowned molars, is square lipped, and is more partial to open countries and grassy valleys, and lives entirely by browsing upon grasses, while the *R. unicornis*, also with hypsodont molars, lives in the upper valleys of India (Assam). We can thus recognize at once the difference in local habitat between the Rhinoceroses with the more primitive cutting teeth of the brachydont type wearing into ridges, and those with more specialized grinding teeth of the hypsodont type of horizontal wear, thickened enamel and cement and numerous secondary folds. In other words, Rhinoceroses occupying the same geographical areas have different local ranges and feeding habits, with which are correlated very pronounced structural differences.

We are accustomed to associate the Rhinoceros with warm climates, but the latest European form (*R. antiquitatis*), as shown by Brandt (1849, 1864), ranged into sub-arctic regions and fed upon coniferous plants. Thus the Rhinocerotidæ had the capacity of wide geographical range and specific adaptation to extremes of climate as well as to local variations of land and flora. These facts throw a great deal of light upon the habits of the extinct species.

2.—GENERAL HISTORY IN AMERICA.

Compared with the Horses and Tapirs, the true Rhinoceroses had a limited development in the New World; they did not migrate to South America, and in North America they appear to have become entirely extinct at the close of the Miocene, at which period they had reached a very large size, a highly modified structure, and wide distribution over the southern half of the continent from Dakota to Florida; at this time there were in fact four sharply distinguished species, but so far as known only one of them certainly bore a horn. This exception is the so-called *Teleoceras major* Hatcher (1894, p. 236), a Loup Fork type with a rudimentary horn on the tips of the nasals, which is either a distinct type or represents a male of *A. fossiger*. In the Oligocene and Lower Miocene there lived the *Aceratheriinae* and *Diceratheriinae*; in the Upper Miocene the *Aceratheriinae* multiplied and ranged in great herds, as we gather from the extreme abundance of their remains in certain localities in northern Kansas, such as the quarry at Long

Island, Phillips Co., Kansas. These *Aceratherium* (*Aphelops*) *fossiger* bone beds are rich in remains, and have already supplied four museums with nearly complete skeletons besides quantities of skulls. It is difficult to explain the apparently sudden extinction of this group on this continent. It may have been the non-development of horns as means of defence against the larger Felidæ, especially the Sabre-tooth Tigers, for all the long persistent Rhinoceroses acquired horns. Somewhat against this conjecture is the fact that hornless types persisted into the Pliocene of India in competition with numerous horned types and equally exposed to the attacks of the large



UPPER MIOCENE ACERATHERE.

Figure 15. Restoration of *Aphelops fossiger*, from materials in the Museum of Comparative Zoölogy, Harvard University. After Scott and Osborn (1890). This restoration is erroneous in the chest region, the ribs being represented far too short.

felines. The cause of extinction does not appear to have been severity of climate, for in the overlying Pliocene or Blanco Beds of North America we find a profusion of animals adapted to a warm climate, but no Rhinoceroses.

Discovery.—In 1850 the first true Rhinoceros was discovered in this country, the well-known *Aceratherium occidentale* from the White River, or Oligocene of Dakota; Leidy (1850-51) originally referred it to *Rhinoceros*, but later finding that the nasals were smooth he referred it to Kaup's genus *Aceratherium*, and gave a very complete description of the skull in his memoirs of 1853 and 1869. In 1858 he reported a single isolated molar tooth as the type of the *R. crassus* from the Upper Miocene or Loup Fork

of Nebraska; in 1865 he described the lower jaw of *R. hesperius* from southern California, and of *R. meridianus* from Texas; in 1871 the *R. pacificus* was described as the first form known from the Lower Miocene of Oregon (John Day). Unfortunately three of these earlier types were isolated and imperfect molar teeth. Among Leidy's latest palæontological labors were his descriptions of the *R. proterus* and *R. longipes*, from the upper Miocene of Florida, species which prove to be identical with Cope's *A. fossiger* (Leidy's *R. crassus*) and *A. malacorhinus*. In 1870 Marsh reported a posterior molar from the Miocene of New Jersey, as *R. matutinus*; in 1873 he described a species from the Pliocene of Oregon, as *R. oregonensis*, and in the same year *R. annectens* from the Miocene of Oregon. In 1875 he referred two more species from Oregon to his new genus *Diceratherium*, namely *D. armatum* and *D. nanum*. In 1873 Cope described the remains of *A. mite*, the oldest known species, from the Lower Oligocene, and in the same year began to fully characterize the imperfectly known Upper Miocene Rhinoceroses by the examination of complete skulls and feet, placing them in the new genus *Aphelops*. In 1879 Cope clearly distinguished four upper Miocene species from each other by marked differences, both in the skeleton and feet, namely, *A. megalodus*, *A. fossiger*, *A. malacorhinus* and *A. superciliosus*. In 1880, he proposed the genus *Peraceras* for the type (*A. superciliosus*) in which the upper incisors had entirely disappeared. In 1890 Osborn and Scott described the skeleton of *A. fossiger*, and gave a complete restoration of this animal from materials in the Harvard Museum of Comparative Zoölogy. Collectors from the Kansas University and American Museums have secured materials sufficiently complete to mount this animal. The next advance came in 1891 with the discovery, by the American Museum expeditions, of a large number of new species, characterizing different levels of the White River Beds, namely, *Aceratherium trigonodum*, *A. tridactylum*, *A. platycephalum* and *A. copei*. The cranial and dental characters were fully described in 1894 by Osborn and Wortman. Finally, in 1893, the Princeton parties secured, from the Loup Fork exposure of the Niobrara River, the skull described by Hatcher as *Teleoceras*. Altogether, twenty Oligocene and Lower and Upper Miocene species of *Aceratherium* have been named or described, and among them we certainly find numerous distinct types, the oldest of which possess upper canine teeth.

3. GENERAL HISTORY IN EUROPE.

The Early Tertiary Rhinoceroses.—Little is known of the structure of the oldest Rhinoceroses of Europe, but the important fact is now established that in the Middle and Lower Oligocene the Rhinoceroses suddenly appear in

species of a similar size and strikingly similar in their premolar structure to the oldest American forms. As the Phosphorites of Quercy were deposited throughout the Oligocene, and are contemporaneous with the long series of Tongrien, Aquitanian, and even Lower Miocene Beds in other parts of France, we find they contain comparatively recent or Upper Oligocene types, such as *A. lemanense* (see Table) as well as types as old as the Upper Eocene. As Mme. Pavlow (1892, p. 191) has clearly shown, it is a decided error upon the part of Lydekker and others, to identify the simple Upper Eocene types of premolars and molars, found in the Phosphorites, with Upper Oligocene species such as *A. croizeti* and *A. lemanense*.

1. They represent the oldest European Rhinoceroses known, and may be readily distinguished by the fact that the premolars are much simpler than the molars, the transverse crests being confluent internally. 2. These premolars correspond with those in Leidy's type of *A. occidentale* from our Middle Oligocene, or base of the Oreodon Beds. 3. The same premolars are therefore more modern in structure than those of *A. mite* or *L. trigonodum* from our Lower Oligocene or Titanotherium Beds. 4. Professor Gaudry, however, describes¹ a still simpler premolar from Quercy, in which the posterior premolar crest is rudimentary, and the tetartocone is united with the anterior crest or protoloph as in *A. copei*. He believes that these oldest types of Europe, like those of America, will be found to possess upper canines. 5. None of these forms have been specifically defined, the remains are so scattered and indeterminate. But Mme. Pavlow mentions other types found at Ferté-Alais of the Middle Oligocene by M. Chalmas, and rightly observes that the two molars from the Upper Eocene of Bach, Switzerland, figured as *A. croizeti* by Lydekker² (1886-82, p. 142), belong in the same primitive class, and not to *A. croizeti*, which is an Upper Oligocene species.

It is thus demonstrated that the American and European Rhinoceroses simultaneously appeared in the Upper Eocene or Lower Oligocene periods of Central Europe and North America, in a very similar stage of evolution, having migrated from some other region. Some precaution is necessary, however, in accepting these older molar teeth of Europe as those of true *Aceratheres*, for it is quite probable that the *Amynodons* also existed there, because the presence of *Cadurcotherium* (certainly a member of the *Amynodontidæ*) in the Phosphorites indicates that this para-rhinoceros also lived in Europe. Rutimeyer (1862), has figured teeth in his Egerkingen collection very similar to those of *Amynodon* (*Lophiodon rhinoceros*). (See Osborn, 1892, p. 764.)

¹ In a personal letter to the author, dated Nov. 2, 1892.

² Catalogue Fossil Mammalia, British Museum, p. 142, mistakenly referred to *A. croizeti*.

The later Tertiary Rhinoceroses.—In the Miocene and later beds we meet with the rich series of species with which the names of Pomel, Kaup, Lartet, Christol, Aymard and Duvernoy, authors of the post-Cuvierian period, are associated. Many of the Pliocene and Pleistocene Rhinoceroses were discovered and defined by the older authors, Blumenbach and Cuvier. About the middle of the century the Pikermi or Upper Miocene types were described by Wagner (1837), and the fossil Rhinoceroses and Aceratheres of Asia from the Siwalik Hills were made known by Falconer (1837) and Cautley. The original confusion in the specific nomenclature has been to a certain extent cleared up by the efforts of Kaup among the Upper Miocene forms, and of Falconer and Boyd Dawkins in the Pliocene and Pleistocene. There long prevailed a tendency to put patriotism before priority in the use of names, as Falconer has observed, and the Woolly Rhinoceros, for example, is still known as *R. tichorhinus* Cuvier west of the Rhine, and as *R. antiquitatis* Blumenbach to the east.

The greatest source of confusion now persisting is in the absence of strict adherence to the *original type characters*. There exist in the case of many species, the 'real type' of the author, and the 'traditional type' of subsequent literature, perhaps a wholly different animal. Therefore the whole literature upon European Rhinoceroses is still subject to revision. In some cases, however, general usage should prevail over arbitrary laws. We hesitate to follow Boyd-Dawkins (1867) and Lydekker (1886-82) in substituting *R. megarhinus* for Cuvier's appropriate term *R. leptorhinus*, "*le Rhinoceros-a-narines noncloisonnées*," on the ground that there is considerable uncertainty as to Cuvier's type. This term (*R. leptorhinus*) was preoccupied by Cuvier and could not be subsequently employed for another species by Owen; we therefore should adopt the *R. merckii* as used on the continent in preference to the *R. leptorhinus* (nomen nudum) as used by Owen.

We owe chiefly to Kaup, Duvernoy, Depéret, Gaudry and Pavlow, our knowledge of the structure of the Miocene Rhinoceroses. Kaup (1862, pp. 4-7) especially has enabled us to utilize the valuable plates of De Blainville's 'Ostéographie' by a complete revision of De Blainville's wholly incorrect system of nomenclature, but the same author greatly erred in placing several quite distinct species from Sansan, Simorre and Eppelsheim together. In Falconer's Memoirs we find the Pliocene and Pleistocene Rhinoceroses treated in a masterly manner. Brandt has given us the most complete account of *Elasmotherium*.

While the Horses, if anything, were more diversified in America than in Europe, the Rhinoceroses reached their highest diversity and development in the Old World. Diverse horned and hornless types in the late Tertiary roamed all over Europe. In the Pleistocene the climax of specialization was reached in the *R. antiquitatis* of Central Europe, and the *Elasmotherium* of

Northern Asia. These became extinct, and the living species of Asia and Africa are descended from less modified Miocene and Pliocene types by links which are as yet only partly determined.

The Aceratheria of Europe are distinguished from those of America by the fact that after giving rise to the one-horned and two-horned Rhinoceroses, they persisted contemporaneously with the horned types as late as the Siwalik deposits. In these remarkable beds are found associated the hornless, the two-horned, and the earliest known single-horned types of Rhinoceroses ancestral to the living Asiatic types. As Falconer has observed (Memoirs, Vol. II, p. 261), the later Aceratheres of Europe were distinguished not only by the non-development of horns, but by many conservative features in the molar teeth, such as: *a*, traces of the external cingulum; *b*, of a well-developed parastyle; *c*, of the antecrochet, which we find even in the Pliocene Siwalik species; *d*, the late retention of the fifth digit in the manus.

It is probable that, excepting the Diceratheres, all the Oligocene and Lower Miocene types of Europe were hornless, for although there was probably a rudimentary horn, the nasals appear nearly smooth in the *R. aurelianensis* of the Sables de l'Orléanais, Lower Miocene. But there are well-developed nasal and frontal horns upon the *R. sansaniensis* of Sansan, an Upper Miocene deposit corresponding to our Loup Fork, and distinctly horned nasals are exhibited in the slightly more recent *R. simorreensis*. Even after the appearance of these horned types, in the Lower Pliocene of Eppelsheim and Pikermi there existed the large *Aceratherium incisivum*, in which the nasals were rapidly degenerating. The full treatment of these animals will be reserved for the third part of this Memoir.

4.—MORPHOLOGY OF THE RHINOCEROS MOLAR TEETH.

Like most other fossil mammals, the Rhinoceroses are chiefly known and distinguished by the characters of the teeth. The more variable incisors and canines have been largely used in definition and classification, but, as with the Titanotheres, the inconstant number of these teeth when in process of reduction, diminishes somewhat their taxonomic value. In the grinding teeth are many stable and constant characters, both the premolars and molars being highly distinctive in their evolution.

Cuvier, Christol, Falconer, Busk, Boyd-Dawkins, Flower and Lydekker, have made the molar differentia a systematic study. This diversity of authorship accounts for the variety of languages from which the terms applied to different portions of the teeth have been derived, as set forth in the accompanying table. The terms were also applied before the uniform

TABLE SHOWING THE TERMINOLOGY OF THE MOLAR TEETH.

	<i>For all Ungulate Molars.</i> Terminology based upon evolution from a Tritericular, bu-nodont, ancestral molar type.	<i>Rhinoceros Molars.</i> Terminology used by English authors, Boyd-Dawkins (1867), Busk (1877) and Lydekker (1882), Foote (1874).	<i>Rhinoceros Molars.</i> Terminology used by Cuvier (1836), De Blainville (1846), Gaudry (1878), Pavlow (1892).	<i>Rhinoceros and Ungulate Molars.</i> German and Russian authors, Rüttimeyer (1863) and Kowalevsky (1873).	<i>Horse Molars.</i> Huxley (1876) and Lydekker (1886, p. 67).
Primary Molar Cones.	{ Protocone { Paracone { Metacone { Hypocone Second costa Costæ (in part)	Denticule interne du premier lobe " externe " " second lobe " " interne "	Innenpfeiler des vorjochs. " Innenpfeiler des nachjochs.	Anterior pillar. Anterior crescent. Posterior crescent. Posterior pillar.
Premolar Cones. ¹	{ Protocone. { Deuterocone. { Tritocone. { Tetartocone.				
Secondary Pillars or Styles.	{ Parastyle { Mesostyle { Metastyle { Hypostyle	First costa = Buttress. " Posterior collis (in part)		Pericones, Randgipfel " " "	Anterior ridge. Middle ridge. Posterior ridge. Posterior prominence.
Secondary Crests.	{ Ectoloph { Protoloph { Metaloph	External lamina = Dorsum Anterior collis Median collis " = Crête externe Colline seconde = Crête ou lobe antérieur La troisième colline = " " postérieur	Aussenwand. Vorjoch. Nachjoch.	
Valleys.	{ Mediusinus { Postsinus	Anterior valley Posterior valley	Vallon oblique. Fossette postérieure.		
Secondary Folds.	{ Crochet { Antecrochet { Crista	Posterior combing { Uncus. plate = { Crochet " = Antecrochet Anterior combing plate = Crista = Crochet. " = Crochet antérieur. " = (Ante-crochet).		
Secondary Pits.	{ Pre-, Medi-, and Postfossettes.		Fossette postérieure = Fossettes.		Cement Lakes.
Cingulum.	{ Cingulum	Posterior collis (in part) = Cingulum, Guard	Bourrelet	Wulst.	

¹ Terminology proposed by W. B. Scott.

derivation of all ungulate and unguiculate molars from tritubercular and sextitubercular ancestors was discovered or even suspected. We can retain only the 'crochet' and 'fossette' of Cuvier; we may substitute 'cingulum' for 'bourrelet,' and 'loph' for 'colline' or 'collis,' and distinguish the three inner valleys as 'presinus,' 'medisinus' and 'postsinus.'

The Latin terminology introduced by Brandt: Collis anterior, Collis medius, Collis posterior, Vallis anterior, Vallis posterior, was an attempt at uniformity, but it is to be rejected for the reason that molar elements having an entirely different history are given the same terms. The terms used in the description of the Horse molar undoubtedly present an equally great diversity in different languages. The uniform terminology proposed by the present writer has been developed in a series of papers (1888, 1; 1888, 2; 1892), and by Scott (1895) as applicable to the molars and premolars of all Ungulates, in fact to the grinding teeth of all the Mammalia.

As is always the case, the highly complex recent forms of molars are rendered comparatively simple to the student by advancing step by step from the earliest types and noting how primitive structures are dropped along the route of evolution, and secondary characters are acquired one by one. The Rhinoceroses were polyphyletic, and among the numerous branches we naturally find great contrasts in the rate of progression or modernization; for example, the most specialized molar types are not found in the modern species, but in the large Pleistocene species, and side by side in Africa live the primitive 'brachydont' *R. bicornis* and the progressive 'hypsodont' *R. simus*. As the modern *R. sumatrensis* skull is in several respects more primitive than that of many extinct Miocene types, so its teeth are much more primitive than those of many ancient fossil teeth. We therefore have to study the teeth irrespective of geological age, and purely from the morphological standpoint, in all the stages between the most primitive and most modified type.

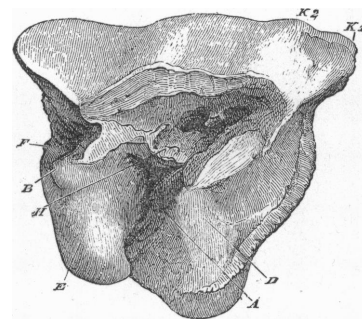


Figure 16. Second right upper true molar of *Rhinoceros megarhinus* illustrating the former system of nomenclature. *A*, median valley. *D*, anterior, and *E*, posterior collis; *F*, posterior valley; *H*, crochet, *K*¹, *K*², first and second costæ. After Lydekker (1886, p. 116).

1.—THE PRIMITIVE MOLAR.

The primitive rhinocerotine type, as we have seen on page 87, is shared by the early Hyracodonts, Amynodonts and true Rhinoceroses. Its origin and its distinguishing features have been pointed out upon page 88. The upper molars are brachydont and have a truncate, wedge-shaped outline, the pos-

terior half of the crown being narrower than the anterior. The ectoloph is divided by three vertical ridges (the 'costæ' of Busk), which, as unknown to Busk, are respectively the remnants of the convex cones of the parastyle, paracone and metacone; the 'costa' of the metacone being the least strongly marked and first to disappear. We notice that the long posterior portion of the ectoloph (evolved from the metacone) is gently concave and slopes inwards; we find vestiges of a primitive external cingulum near its base. The cingulum entirely invests the anterior, posterior and internal bases of the crown. The two transverse crests are perfectly simple and incline slightly backwards. The fact that the protoloph is always longer than the metaloph is due to persistence of the primitive triangular or tritubercular contour of the ancestral bunodont molar.

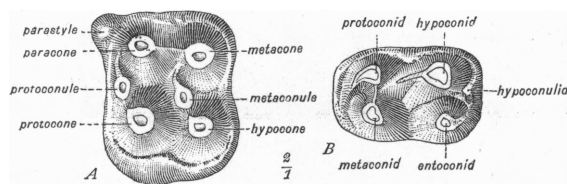


Figure 17. Superior and inferior molars of *Hyracotherium vulpiceps*, showing primary cones in bunodont stage. After Owen (1858).

compare the action of the Rhinoceros grinders with those of the Horse we shall find that the lower molars of the Horse sweep across the entire crown of the upper molars; but in the 'brachydont' Rhinoceros molars they sweep mainly across the inner side, which is usually worn deeper than the outer wall, the crowns wearing into ridges. This simple fact probably explains why the outer enamel of the rhinocerotine ectoloph early lost its primitive folds when they were no longer of service, while the inner enamel of the ectoloph and the sides of the two transverse crests acquired several secondary folds.

The four extreme or final adaptive tendencies are then: 1. Vertical elongation of the crown, accompanied by partial loss of the basal cingulum, thickening of the enamel, and upward growth of cement. 2. Straightening or flattening of the outer enamel wall of the ectoloph. 3. Folding of the inner enamel wall of the ectoloph and of the

This original rhinocerotine type is essentially a *brachydont cutting tooth*, and the extreme tendency of Rhinoceros evolution is to produce out of this a *hypsodont grinding tooth* which will withstand prolonged horizontal wear and break the food up into fine particles, facilitated, as in the Horse molar, by a *folding of the enamel* upon the entire crown. If with Ryder we

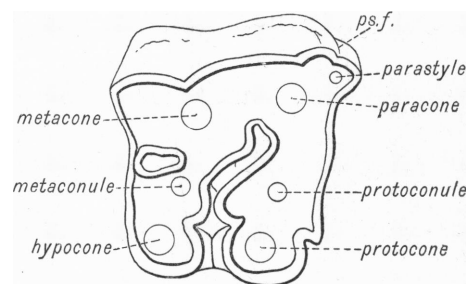


Figure 18. Diagram of superior molar of *A. (Peraceras) superciliosum* showing relation of primary cones as growth centres to secondary folds.

enamel of the protoloph and metaloph. 4. Elevation of the posterior basal cingulum, as in the Horse, and extension of the posterior region of the crown to produce an additional folded surface around the postfossette. 5. Substitution of the horizontal wear of a 'hypodont' crown for the oblique wear of a 'brachyodont' crown.

COMPARISON WITH THE EVOLUTION OF A HORSE MOLAR.

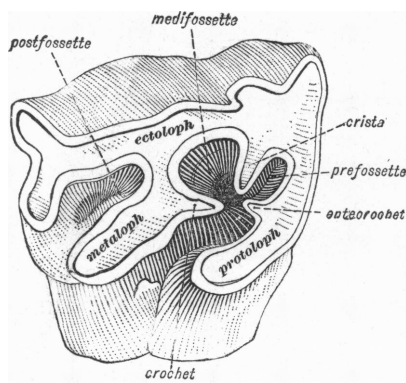


Figure 19. Diagram of typical superior molar (or milk molar) showing all the secondary folds. After de Blainville, 'Ostéographie,' Rhinocéros (Strasbourg), Plate XIII.

If we compare the molars of a Rhinoceros with those of an Upper Miocene Horse, such as *Merychippus*, we see that a number of very similar features are acquired. (See Osborn, 1893, p. 208.) No mesostyle is found in the primitive Rhinoceros, but the 'crista' is analogous to it, and compensates for it; the protoconule sends back an 'antecrochet' in both Horse and Rhinoceros, and the posterior cingulum rises as the hypostyle in both. Therefore there is a striking likeness between the 'fossettes' of the Rhinoceros tooth and the 'cement lakes' of the Horse tooth; they are, in fact, homologous. (See Table, page 104.)

There are many further analogies with the evolution of the Horse molar which we shall point out later. Unlike the Horse molar, the foldings are not uniformly produced, but display wide variations which are of great value in taxonomy as utilized especially by English authors, and which deserve the closest study. It is the neglect of these important and slowly acquired folds which has caused Kaup and other continental palæontologists to place together a number of distinct species.

SEQUENCE OF MOLAR EVOLUTION.

The parts are affected as follows:

1. The cingulum disappears first upon the convex portions of the ectoloph, then upon the entire ectoloph; these steps can be seen upon the molars of different species of *Aceratherium* from the Oligocene and Lower Miocene, yet a strong cingulum is seen

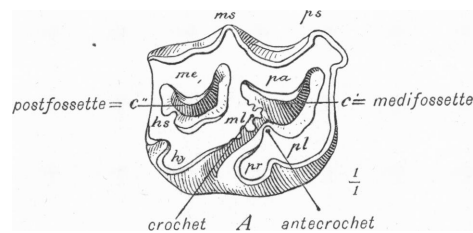


Figure 20. Right superior molar of *Merychippus insignis*, after Leidy (1896, Plate XVII. Regarded by Cope as a milk tooth). This figure shows that the anterior and posterior cement lakes, *c'*, *c''* are equivalent to the fossettes of the Rhinoceros molar, and that the folds from the protoloph and metaloph arise from the same regions as the crochets of the Rhinoceros molar. The mesostyle, *ms*, is a structure which has no homologue in the Rhinoceros molar.

around the crown of the Upper Miocene *R. brachypus*, and recurs upon the inner side of *R. antiquitatis*. (See Diagram, Fig. 21.)

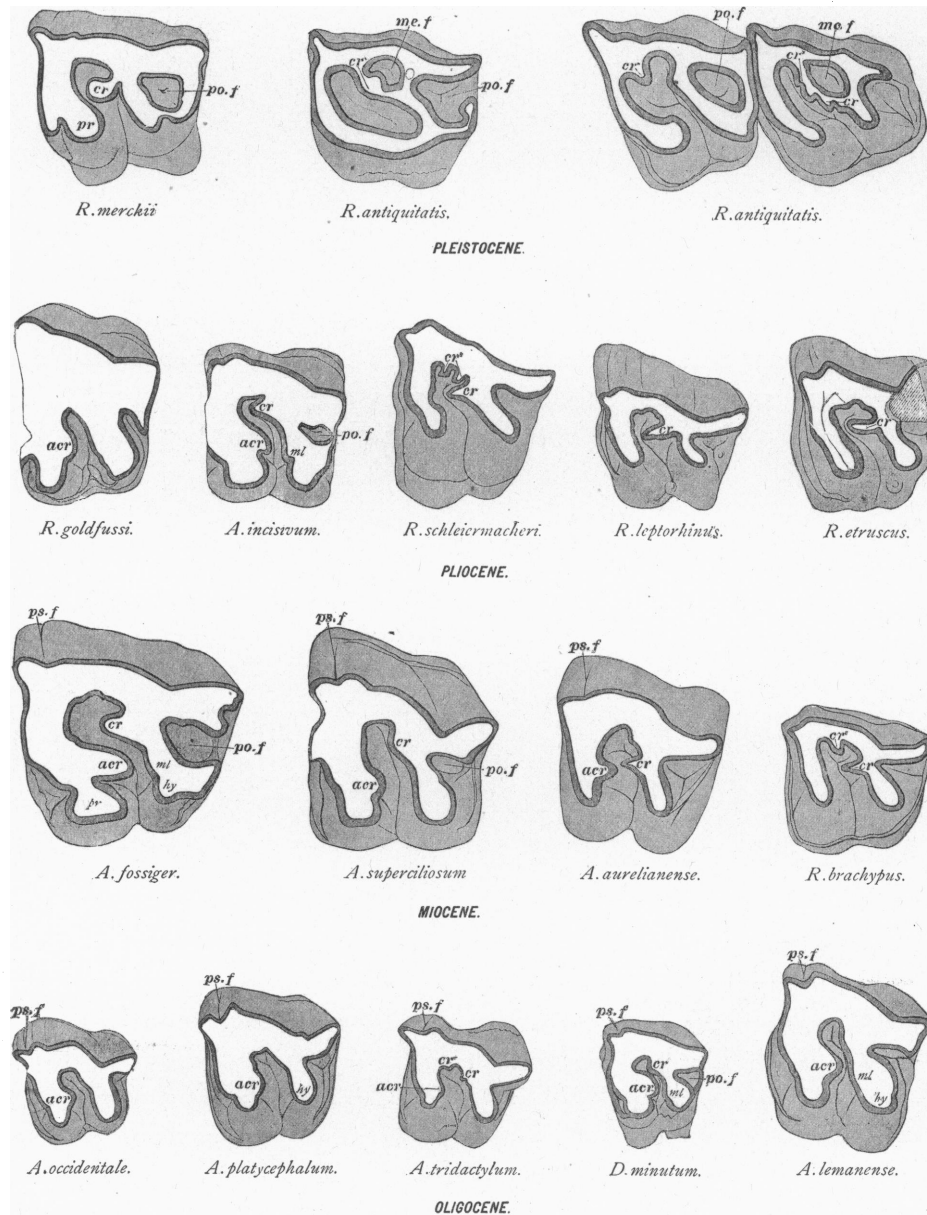
2. Typically the inner side of the crown loses its cingulum, which often leaves a 'cingule,' or 'median tubercle' at the entrance of the median valley, as in the *Diceratherium* of Oregon, or in *R. leptorhinus*. Then the anterior cingulum disappears as in *Aceratherium fossiger*, and lastly the posterior cingulum either disappears or is elevated in the mid-region and unites with the hypostyle to form the hinder wall of the 'postfossette' (*A. fossiger*, *A. incisivum*, *R. merckii*, *R. antiquitatis*, etc.), an evolution which corresponds to the development of the hypostyle in the Horse molar. This crest, exactly analogous to that which appears in the Horse, *is not to be compared* with the main transverse proto- and metalophs, yet the term 'collis posterior,' applied to it by Brandt and other authors, would imply some ground for such comparison.

3. The four stages in the flattening of the outer face or wall of the *ectoloph* are also shown in the Diagram on page 109, especially the disappearance of the deep fold, *ps.f.*, between the parastyle and paracone. The first to disappear, in the Eocene, is the convexity of the metacone, or one of the 'posterior costæ' of Busk and Boyd-Dawkins. During the Miocene we observe the flattening of the paracone, or 'median costa.' In the Upper Miocene (*Aceratherium fossiger*) the 'anterior costa,' or remnant of the parastyle, follows suit and disappears. This 'buttress,' as Flower and Lydekker have termed it, persists in many recent species, and there are only a few forms in which the final stage of its disappearance is reached; among them are *R. palæindicus*, *R. leptorhinus*, and the later Pleistocene Rhinoceroses of Europe, such as *R. merckii* and *R. antiquitatis*.

4. The earliest secondary fold to appear is the 'antecrochet,' a projection from the *protoloph* into the median valley. This 'antecrochet,' as Gaudry has rightly pointed out (1878, p. 58), seems to be a spur from the primitive *protoconule* (denticule interne du premier lobe); it is faintly indicated in all the Eocene, and strongly developed in all the Oligocene Rhinoceroses of America and Europe; it persists in *A. incisivum*, *R. schleiermacheri*, and other Lower Pliocene forms of Europe, and is also found in some of the American Upper Miocene Rhinoceroses, but it is a singular fact that it is absent in all the European and Asiatic Rhinoceroses, from the Upper Miocene period onward to the most recent forms.

5. In looking over large series of teeth of all ages, there is no doubt that the outer and anterior portion of the crown, including the *ectoloph* and the entire *protoloph*, tends to become progressively simpler, and that the later secondary foldings are mainly in the posterior portion of the crown. Thus the

Figure 21. DIAGRAMS SHOWING THE EVOLUTION OF THE RHINOCEROS MOLARS.



EXPLANATION.

OLIGOCENE RHINOCEROSES show the 'antecrochet' (*a.cr.*), 'parastyle fold' (*ps.f.*), the 'metaconule fold' (*ml.*), and in some cases rudiments of the 'crochet' (*cr.*).

MIOCENE RHINOCEROSES show both antecrochet and crochet remains of the 'parastyle fold' and 'metaconule fold,' rudiments of the 'postfossette' (*po.f.*) and *crista* (*crs.*).

PLIOCENE RHINOCEROSES show remains of the antecrochet and usually a strong crochet. Postfossette, 'metaconule fold' and 'crista' variably developed and constituting specific characters.

PLEISTOCENE AND RECENT RHINOCEROSES invariably show the crochet. Medifossette (*m.f.*) sometimes developed. Postfossette and *crista* constituting specific characters.

metaloph in the *Aceratherium incisivum* of Europe develops a sharp forward spur, the 'crochet'; this is always nearer the head of the valley than the 'antecrochet,' and often arises from the junction of the ectoloph and metaloph, as in *A. fossiger*; in such types it may be mistaken for the 'crista' (Hatcher, 1894, p. 242). Gaudry (1878, p. 58) has mistakenly traced its origin to the metaconule, but from this element the temporary 'metaconule fold' arises. In the *A. lemanense* of Europe this 'crochet' is faintly developed, but in every other known species above the Lower Miocene it is strongly developed, and is therefore one of the most characteristic and least distinctive features specifically.

6. In *Hyrachyus* and in the Middle Miocene *Diceratherium* and *Aceratherium*, and in many later Old World forms, the inner wall of the ectoloph

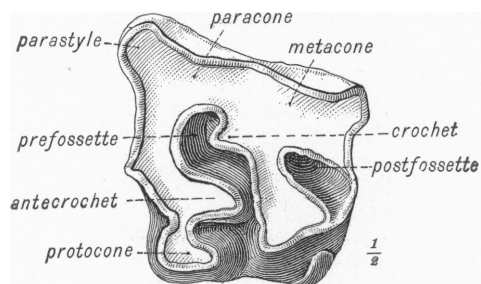


Figure 22. Left superior molar of *A. (Aphelops) fossiger*, showing secondary folds. Collection Mus. Comp. Zool., Harvard University.

develops a secondary fold called the 'crista' or 'combing plate,' which projects into the head of the medisinus; in the permanent molars it is usually single, but in certain species (*R. schleiermacheri*) and in many milk molars we see a number of 'cristæ.' This fold is somewhat variable, but is of distinctive specific value. In certain Pleistocene and other types it unites with the 'crochet.'

7. The internal portion of the protocone often exhibits a decided constriction of the protocone, reminding us of a similar character in the Palæotheres and Horses; this constriction is especially marked in *A. fossiger* (see Fig. 22). In certain Oligocene species, but most clearly in *A. megalodus* and *A. incisivum*, the hypocone is also constricted, bringing the metaconule into prominence, *ml.* This fold, however, does not develop, and is not to be mistaken for the true 'crochet' which arises near the ectoloph.

8. The fourth step in secondary folding affects the metaloph. The inner end of the metaloph frequently unites with the posterior cingulum (*e.g.*, *A. fossiger*), and develops a recurved spur which extends outwards; a similar spur is sent inwards from the end of the ectoloph, thus the 'posterior fossette' is partially enclosed, as in *A. fossiger* and *A. antiquitatis*.

9. The three 'fossettes' are important features of later molar evolution; the posterior, or 'postfossette,' as just described, is a sub-circular valley behind the metaloph in the posterior region of the crown; a comparison of *A. occi-*

dentale and *R. antiquitatis* shows that this broad region is a new development, for there is only a very narrow space between the metaloph and posterior border in the primitive molar. This supports a remark made above (under 7), as to the evolution of the posterior portion of the crown. The middle or 'medifossette' is formed¹ by the junction of the 'crista' and 'crochet' after prolonged wear, while the 'prefossette' forms in the angle between the 'crista' and protoloph. As the third or posterior molar usually lacks the posterior valley, only the two anterior 'fossettes' can be formed; an exception to this is, however, seen in *R. antiquitatis* and *R. sinus*, and perhaps in *A. blanfordi*, in which there is a postsinus and three 'fossettes.' (Falconer, 1868, p. 335; Cuvier, 1836, Oss. Foss., Pl. VI, Fig. 4.)

10. The large upper tooth of *R. antiquitatis* from the Pleistocene of Kent, England, presents almost the final stage of molar development, as described by Owen and Lydekker. The enamel is very thick and rugose; the contour is subquadrate; there is no distinct cingulum upon either the external, anterior or internal faces. The ectoloph is nearly straight, with no trace of the parastyle, it is greatly produced backwards; there is a large 'crista,' and three 'fossettes' are formed upon the worn crowns. The crowns of the upper and lower cheek-teeth are worn nearly horizontally.

11. The final stage of evolution is exhibited by *Elasmotherium*, in which the enamel of the entire tooth is thrown into a series of sinuous folds (Fig. 24).

12. Depéret (1885, p. 268) has pointed out that the addition of *cement* and the *secondary oblique* position of the molar crests furnish important criteria in the distinction of the Rhinoceroses. He has accordingly grouped the Old World types as follows:

I.	II.	III.
Upper molars with cingulum, and broad lochs with a simple 'antecrochet,' without cement.	Cingulum reduced. Enamel smooth. A forked 'crista' and 'crochet.' Transverse lochs perpendicular to ectoloph. A cement layer.	Molars laterally compressed. Transverse lochs very oblique to ectoloph. Enamel and cement layers very thick.
<i>A. lemanense.</i> (<i>A. randanense.</i>) <i>R. brachypus.</i> <i>A. tetradactylum.</i> <i>A. incisivum.</i> <i>A. goldfussi.</i>	<i>R. schleiermacheri.</i> <i>R. pachygnathus.</i> <i>R. leptorhinus.</i> <i>R. etruscus.</i> <i>R. hemitechus.</i> <i>R. bicornis.</i>	<i>R. antiquitatis.</i> <i>R. sinus.</i>

¹ See Figure of *R. antiquitatis* in Lydekker, Brit. Mus. Cat., pt. III, p. 93.

13. The *third upper true molar* has a different course of evolution of its posterior region, because of the union of the ectoloph and metaloph to form a single oblique crest. As an exception to this union Falconer observes that the last upper molar sometimes presents the most pronounced characters for distinguishing species; he points out that in *R. simus* and *R. antiquitatis* this tooth has a posterior valley, that is, the ectoloph and metaloph are not confluent, whereas in all other Pliocene and recent Rhinoceroses they are. Otherwise in the disappearance of the external folds and acquisition of secondary internal folds, the third molar follows the same laws as its fellows, but is always more retarded than m_1 and m_2 .

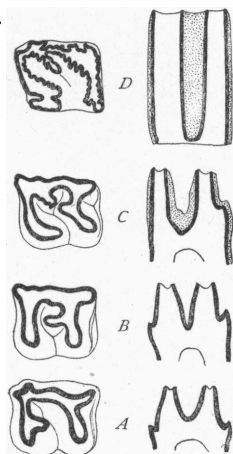


Fig. 23. Diagram of stages in hypsodontism and deposition of cement. Superior molars of A, *Aceratherium lemanense*; B, *Rhinoceros pachygnathus*; C, *Rhinoceros antiquitatis*; D, *Elasmotherium sibericum*. After Gaudry and Boule (1888, Pl. XVIII).

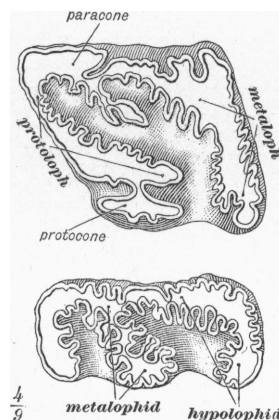


Figure 24. *Elasmotherium sibericum*. Superior and inferior molars. After Gaudry and Boule (1888, Pl. XVII).

SUMMARY OF MOLAR EVOLUTION.

<i>Primitive Form.</i> EOCENE.	<i>Intermediate Form.</i> OLIGOCENE.	<i>Extreme Modification.</i> PLEISTOCENE.
Brachyodont. Crown narrow posteriorly. Cingulum vestigial on outer side. Enamel thin, smooth. Ectoloph oblique. Cones of parastyle, paracone and metacone distinct. Transverse crests simple. Ectoloph and metaloph distinct upon m^3 . Crowns worn obliquely.	Brachyodont. Crown sub-quadrate. Cingulum wanting on outer side, reduced on inner sides. Ectoloph with cones of parastyle and paracone only distinct. Protoloph with antecrochet. Ectoloph and metaloph conjoined in m^3 . Antecrochet and an incipient crista.	More or less hypsodont. Crown quadrate. Extension of cingulum principally on posterior side. Enamel thickened, rugose. Ectoloph with cones of parastyle, paracone and metacone obsolete. Crista and crochet present. No antecrochet. Three fossettes. Cement. Crowns worn horizontally.

PREMOLAR EVOLUTION.

(See Plate XIII.)

The stages in the assumption of the molar pattern by the premolars furnish the key to the Oligocene species of *Aceratheres*, and are thus of great importance.

1. The outer wall or ectoloph of the premolar *primitively* bears two vertical 'costæ,' the 'protocone' and 'tritocone'; to these are added the 'parastyle,' making three vertical ridges as in the molars; but, as the premolars gradually approach the molar pattern the 'tritocone' costa disappears. (Compare Figs. 3 and 8, Plate XIII.) The inner wall of the molar bears a strong internal cingulum (see Figs. 1-10, Plate XIII).

2. The first upper premolar is subject to wide specific variation; it is always small but is sometimes quadrate with two distinct crests (*A. occidentale*, *A. tridactylum*), sometimes elongate and narrow (*A. platycephalum*).

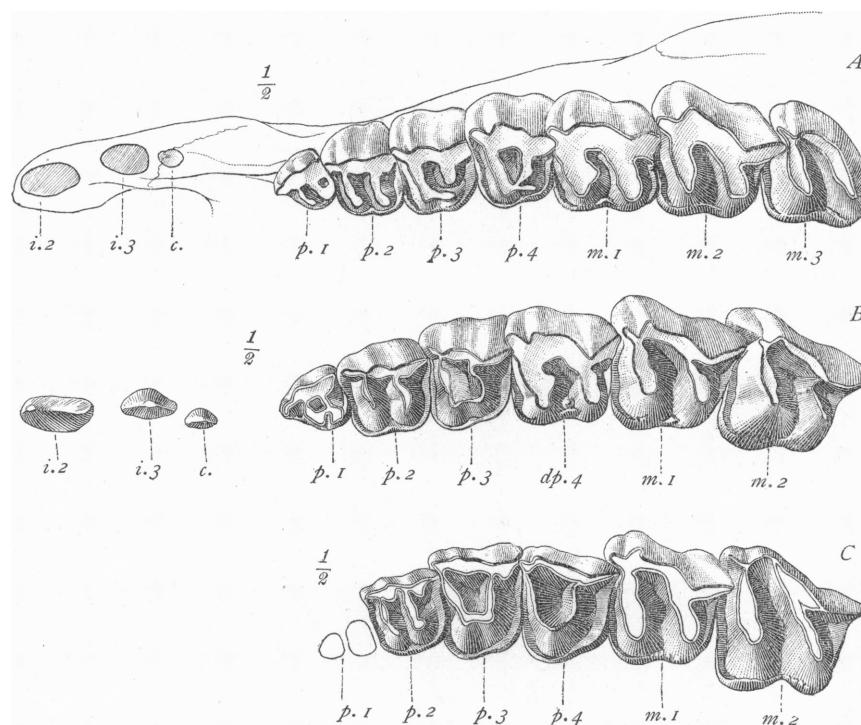


Figure 25. Upper dentition of the left side of: C, *Leptaceratherium trigonodum*, type specimen (No. 528); B, *Aceratherium copei*, showing unworn dentition (No. 521); A, *Aceratherium copei*, showing fully worn dentition (No. 522). Collection of the American Museum of Natural History.

3. The second upper premolar, in all the American Oligocene *Aceratheres* at least, is distinguished by two perfectly distinct transverse crests which are acquired long before the third and fourth premolars acquire two crests. This is a very important and distinctive character of the Rhinoceroses, and it raises the suspicion that the supposed p^2 is really dp^2 , or a persistent milk tooth, but, as discussed on a later page, this is not certainly borne out by a comparison of the deciduous and permanent premolars in *A. copei* and *A. occidentale*, of different ages, which seem to show a precocious replacement of the premolars. The facts support the following law:

In the early true Rhinoceroses the transformation of the premolars into the molar pattern begins with pm^2 , then extends to pm^3 , and finally pm^4 . The first, second, and sometimes the third permanent premolars are precociously developed in some species, and at an early geological period acquire the molar pattern.

The premolar transformation thus extends from before backwards, instead of from behind forwards.

4. The *typical* mode of transformation is well seen in a comparison of pm^3 and pm^4 in all the species illustrated upon Plate XIII. First, the protoloph sends back a hook terminating in the tetartocone. Second, this tetartocone detaches from the protoloph and unites with the metaloph. Third, the 'medisinus' opens between the protoloph and metaloph. This peculiar history explains the closed valley or 'medisinus,' which is found in all worn premolars of the Oligocene period. *Atypically* the tetartocone springs from the metaloph.

5. In loss of primitive characters and acquisition of *secondary* characters the premolars naturally lag behind the molars; they retain the three external ridges longer; the 'antecrochet,' 'crochet' and 'crista' are later in appearing and more irregularly developed; the fourth premolar develops a number of 'cristæ' in some Pleistocene species; the internal cingulum persists as a broad band in certain Miocene and even Pleistocene species.

MILK DENTITION.

1. The deciduous premolars directly reverse the law observed in the permanent premolars, that is: *the posterior milk premolars are more progressive than the anterior, the transformation extending from behind forwards.*

A comparison of Plate XIII, Figs. 5 and 6, of *A. occidentale*, illustrates not only how far in advance of the permanent teeth are the deciduous teeth, but this reversal in the order of evolution.

2. The deciduous premolars in many cases precociously acquire secondary structures which will be subsequently acquired by the permanent molars; they are thus sometimes prophetic of molar development, as in the acquisition of the 'crista' and of the 'antecrochet.'

EVOLUTION OF CUTTING TEETH.

The oldest Rhinoceroses known from the base of the Oligocene are already well advanced in the specialization of the cutting teeth towards the peculiar adaptation of the two large semiprocumbent *lower canines*, which close as a cutting shear upon the outer sides of the two large *second upper incisors*. Hypertrophy of these teeth is correlated with the atrophy of all the lower incisors and of upper incisors i^2 and i^3 , together with the upper canines. This

climax of specialization persists in many lines of descent, while in other lines leading to the atelodine forms all the cutting teeth are gradually atrophied and disappear. It is not probable that the ancestors of the atelodine types ever possessed greatly hypertrophied upper and lower cutting teeth. For it is evi-

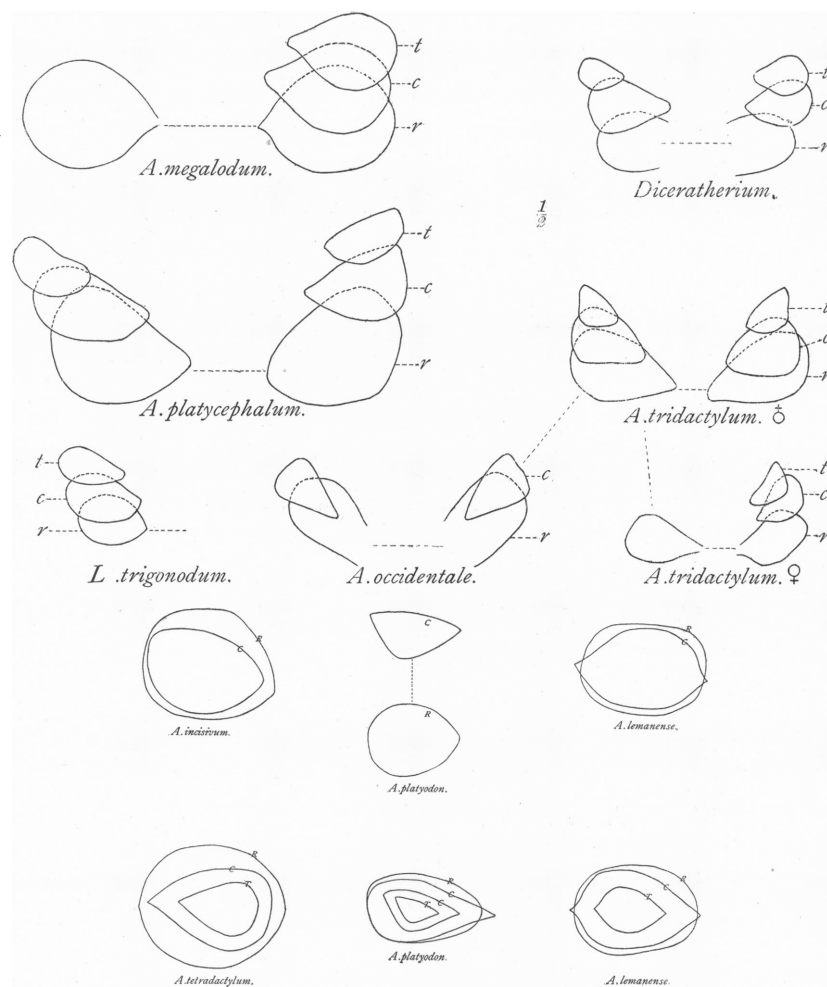


Figure 26. Sections of the inferior canines of several species of European and American Rhinoceroses, showing the three canine types: I. SUBOVAL, with interior acute edge, *A. megalodum*, *A. platycephalum*, *L. trigonodum*, *A. tetradactylum*, *A. incisivum*. II. SUBOVAL, with internal and external acute edges, *A. lemanense*. III. SUBTRIANGULAR, especially towards the apex of crown, *A. platyodon*, *A. tridactylum* and *Diceratherium*.

R, root section; c, mid-crown section; t, terminal crown section. American species original. Foreign species after Mermier (1895, p. 30). All one-half natural size.

dent that when fully developed, as in certain Upper Miocene forms, these teeth were in constant use.

The stages of the loss of the single pair of lower incisors, of the lateral upper incisors, and of the upper canines will be fully described in the succeeding account of the Oligocene forms.

Mermier in 1895 directed our attention to the striking differences of form in the lower canines as shown in transverse sections. It appears from the

writer's studies that these differences partly represent distinct phyletic types rather than successive stages of development of a single type, and will therefore become of considerable value in phylogenetic study. There are first, the oval types, in which the section of the canine shows an internal cutting edge, as seen in *A. trigonodum*, *A. platycephalum* and *A. tetradactylum*. Second, there are the oval types, such as *A. lemanense*, with both internal and external cutting edges. Third, there are the triangular types, such as *A. occidentale*, *A. tridactylum* and *Diceratherium*, and *A. platyodon*. As indicated in the sections of *A. tridactylum* of Fig. 26, there are marked sexual differences in the development of the canines correlated with characteristic smoothness or rugosity of the skull.

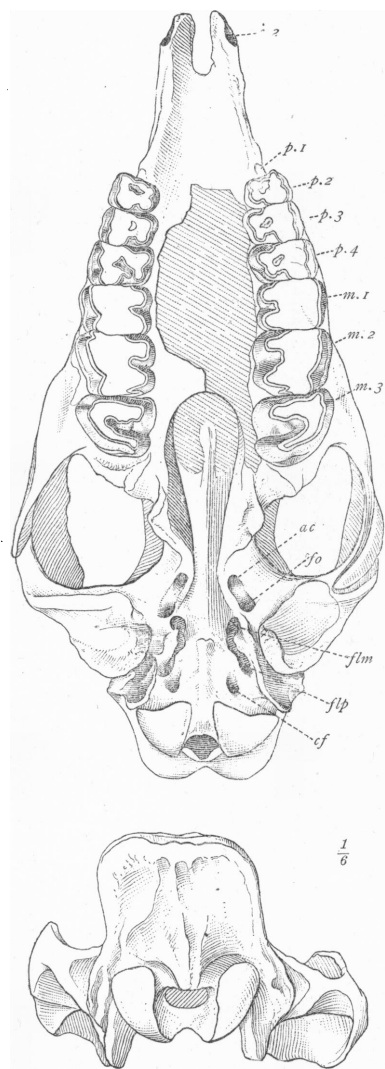


Figure 27. Palatal view and occiput of skull of *Aceratherium platycephalum*, showing separation of the foramen ovale and foramen lacerum medium. Collection American Museum of Natural History (No. 1478).

5.—MORPHOLOGY OF THE RHINOCEROS SKULL.

Leidy, Cope, Flower, Gaudry and many others have discussed the progressive changes in the skull.

Certain features of the primitive Rhinoceros skull persist throughout the subsequent profound changes—these are the opening of the orbits into the temporal fossæ with feeble postorbital processes, and more exceptional than this, the equal development of post- and præ-orbital regions of the skull. The elongation of the molars is not accompanied by an elongation of the face as in the Horses and Ruminants, but by a deepening of the maxillaries for the development of the grinders beneath the orbits.

The earliest departure from the primitive type, in the lower Oligocene, is the deepening of the naso-maxillary notch, the consequent extension of the free portion of the nasals, and separation of the premaxillaries from the nasals (*A. copei*, *A. occidentale*). The loss of the superior cutting teeth, in many Upper Miocene and later types, is followed by the further reduction of the premaxillaries and their separation in the middle line. In most fossil Rhinoceros skulls the premaxillaries are found detached. Thus the disuse of the cut-

ting teeth results finally in the degeneration of the anterior portion of both upper and lower jaws.

This loss is compensated by the remarkable development of the grinders and correlated muscular and cranial modifications, which are well seen in a comparison of all the known *Rhinoceros* skulls. Along the top of the skull the longitudinal suture between the parietals, frontals and nasals disappears from behind forward. The primitively sharp sagittal crest of *Hyrachyus* and the Lower Oligocene species gradually widens out into the supra-temporal ridges, accompanied by a reduction of the *temporal* muscles, employed in the

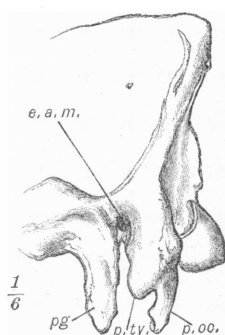


Figure 28. Lateral view of occipital region of skull of *Rhinoceros sumatrensis*, showing primitive backward slope of occiput and open external auditory meatus. After Flower (1876, p. 444).

direct vertical chopping or cutting motions of the jaw in the brachydont types, and an increase of the *masseter* and *pterygoid* muscles employed in the swinging or grinding motions of the hypsodont types. At the same time the coronoid process of the jaw as the chief insertion of the temporal muscle is reduced; the primitively sharp backward angle of the jaw (as seen in *R. sumatrensis*) subsides into the forward sweep of the lower border (as seen in *R. pachygnathus*, *R. simus*, *R. bicornis*, *Elasmotherium*), the post-glenoid process of the jaw is shifted inward so as to give a free universal swinging

motion of the mandibular condyle in the glenoid facet; and correlated with this the strong post-cotyloid process is developed behind the condyle for the attachment of the large suspensory ligament. The post-glenoid process itself is at first low and transverse, as in the Tapir; it has the remnant of this form in *A. occidentale*, but it gradually is shifted to the inner side of the facet and becomes long and triangular in section; in the Upper Miocene Rhinoceroses it is shaped as in the modern forms.

The form of the *occiput* also becomes very characteristic, as shown upon Plate XIX, and in Figs. 28-9. 1. The primitive occiput is both low and narrow, and extends in a *backward oblique plane*, overhanging the condyles. This primitive backward extension is seen in all the Oligocene Aceratheres, and, while the occipital crest broadens above, persists in the Upper Miocene *A. incisivum* as well as the Pliocene and Pleistocene tichorine Rhinoceroses of Europe, and the modern *R. simus* and *R. bicornis*. 2. The second type of occiput is broad, flat, and in *vertical plane* as in *A. fossiger*, *R. aurelianensis*, and *R. sansaniensis*. 3. A third type slopes in a *forward oblique plane* as in *A. superciliosum*, *R. indicus* and *R. sondaicus*. There thus appears to be no correlation between the plane of the occiput and the presence or absence

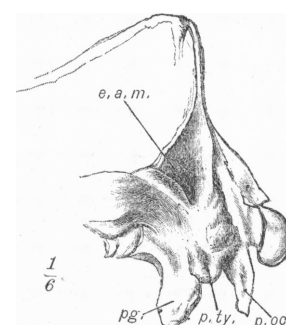


Figure 29. Lateral view of occipital region of skull of *Rhinoceros sondaicus*, showing the forward slope of occiput and the enclosure of the external auditory meatus. After Flower (1876, p. 445).

of horns. The rugosity of the occiput is naturally correlated with the presence of powerful muscles, as in the low rugose occiputs of the two heavily-horned Pleistocene and African species. The form of occiput, however,

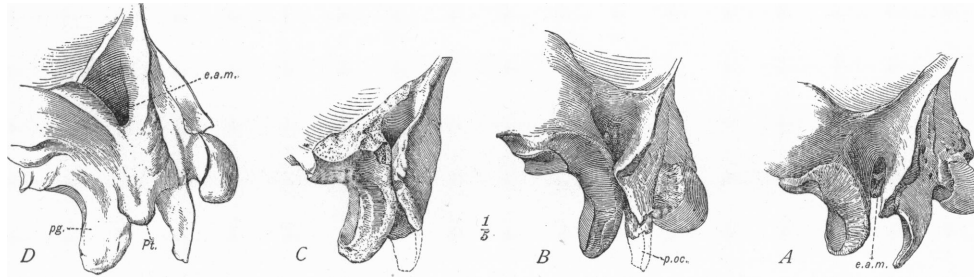


Figure 30. Lateral view of auditory region of four species of Rhinoceroses, showing gradual enclosure of external auditory meatus. A, *Rhinceros sumatrensis*; B, *Aceratherium tridactylum*; C, *Aceratherium (Teleoceras) fossiger*; D, *Rhinceros sondaicus*. After Hatcher.

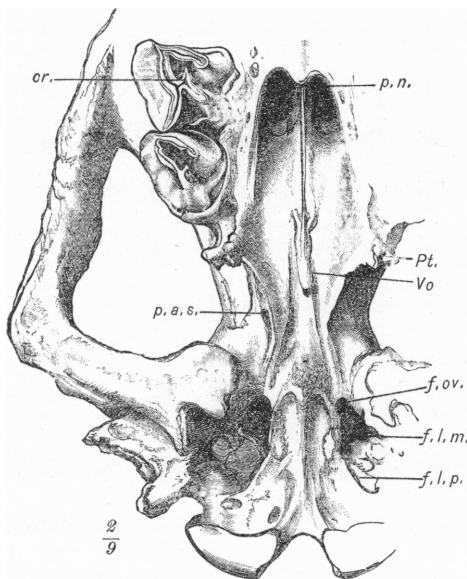


Figure 31. Basioccipital region of skull of *Rhinceros sondaicus*, showing development of 'crochet,' also union of foramen ovale (*f.ov.*) with foramen lacerum medius (*f.l.m.*). After Flower (1876, p. 447).

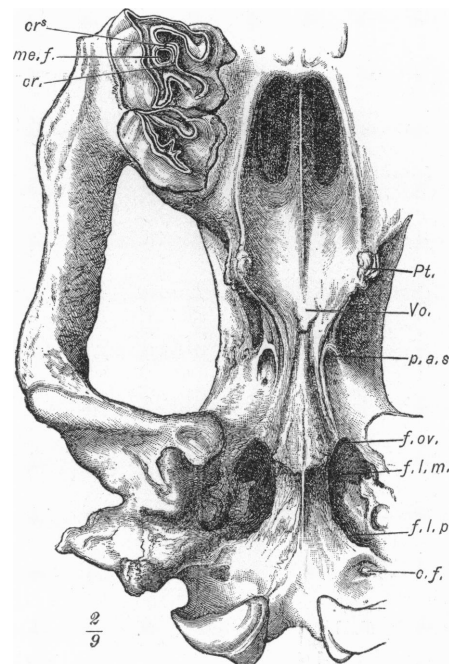


Figure 32. Basioccipital view of *Rhinceros unicornis*, showing union of foramina, and formation of medifossette (*me.f.*) by union of crista and crochet in the molar teeth. After Flower (1876, p. 446).

is correlated with the dolichocephalic and platycephalic skull types, and will become of extreme value in phylogeny.

The vertical flattening of the occiput and general shortening of the post-auditory region of the cranium, is chiefly the cause of the progressive inclosure of the auditory meatus inferiorly by the broad union of the post-tympanic

processes and the posterior portion of the zygomatic arch. This posterior shortening of the cranium is also responsible for another very characteristic feature of Rhinoceros skull evolution—namely, the progressive confluence of the foramen ovale with the foramen lacerum medium, which can be observed in all stages from the Oligocene to the Miocene types. This is preceded by the confluence of the foramen rotundum and foramen lacerum anterius, as observed by Cope (1873, p. 230, also 1879, p. 771c), and Leidy (1869, p. 222). These foramina are separate in *A. platycephalum*, *Aceratherium mite*, and the older types of *A. occidentale*.

In the ancient Rhinoceroses of America there is no diploë; the osseous cranial wall is solid in the Oligocene *Aceratheres* and even in the Upper Miocene *A. fossiger*, which has a remarkably large brain. In the recent Rhinoceroses the form of the brain-case proper is concealed by the expansion of the diploë into extensive occipito-parietal air cells. The brain of the living *R. sumatrensis* is considerably smaller than that of the Upper Miocene *A. fossiger*. The primitive *Aceratheres* are all long-headed or dolichocephalic. Observing the skull of the progressive Rhinoceroses as a whole, we are at once struck by a division of both the hornless and horned series into long, low-skulled, and short, wide-skulled types—namely, into *dolichocephalic* and *brachycephalic* *Aceratheres* and Rhinoceroses. This affords an additional divergent character or clue to the phylogeny of the family, which may prove to be very important.

6.—PRELIMINARY BASIS OF CLASSIFICATION.

The widest difference of opinion and practice prevails regarding the classification of the Rhinoceroses. By Flower (1891) the whole family is placed under the single genus *Rhinoceros*, which is made to embrace forty species, extending from the Eocene period to modern times. By Cope (1879), on the other hand, four sets of characters are taken for generic distinctions, namely: (a) The successive loss of upper and lower incisor teeth; (b) the development of one or two horns; (c) the development of an osseous narial septum; (d) the loss of the fifth digit from the manus. Thus Cope (1879) was led to adopt not less than nine genera, and many more would be added by subsequent discoveries if his quadruple principle of definition should be consistently applied. The writer is not prepared at present to propose a final classification of this group, believing that an ideal classification is an expression of phylogeny, and at present the phylogeny of the Rhinoceroses is so obscure that ideal classification is impossible. The group is full of peculiar taxonomic difficulties, greater than those in any other family of Perissodactyls, and our knowledge of certain forms is still far from complete. For example, it is uncertain whether

Kaup's *Aceratherium incisivum* possessed three or four digits. It probably had three, for the metapodial which he originally believed represented the fifth digit, proved to belong to a Carnivore (See Kaup, 1859). If this is the case there is room for a valid generic separation of Aceratheres with four toes. If, on the other hand, *A. incisivum* was a four-toed type, then there is room for a valid Acerathere genus with three toes, such as Cope's *Cænopus*. This term *Cænopus*, however, is antedated by Aymard's *Ronzotherium*, and no one yet knows whether this Lower Oligocene form of Europe had three or four toes. Under these circumstances the generic term *Aceratherium* is retained in this Memoir for both three and four-toed types of Aceratheres.

Criticism of Cope's and Lydekker's Systems.—It is moreover impracticable to follow Cope in the separation of the Rhinoceroses upon the basis of their homoplastic or parallel progressive modifications. We can only separate them upon their heteroplastic or divergent modifications. The tendency to lose the upper and lower cutting teeth was a family characteristic, which pervaded all branches ; this loss was attained to a greater or less degree in each branch ; it therefore does not distinguish the branches from each other, but rather the successive specific stages within each branch. The *Atelodine Group* of Lydekker (1886, p. 92) therefore (which includes the dolichocephalic *R. antiquitatis* with the brachycephalic *R. pachygnathus*), is an unphilosophical and unnatural group.

The same is true of all the progressive parallel characters enumerated upon an earlier page. We find, for example, that the hornless Upper Miocene *A. superciliosum* has no upper incisors, neither has the heavily-horned *A. bicornis* of Africa. This toothless condition is no proof of any relationship between these two forms, but merely of their family relationship or of the final expression of similar tendencies of adaptation due to their remote community of origin.

When this family is more thoroughly known we shall be able to distinguish the truly divergent characters and separate genera upon a natural basis. At present it seems best to disregard the number of incisor teeth, and base our divisions primarily upon the skull type—whether brachycephalic or dolichocephalic; secondarily upon the horns, and finally upon the molar type. The presence or absence of horns is a progressively divergent feature ; the presence of one or of two horns is less essential, for, as Flower has pointed out, the one-horned Indian species of Rhinoceroses, *R. unicornis* and *R. sondaicus*, are superficially related to each other in the possession of a single horn, but the latter is clearly distinct from the former, and closely allied to the two-horned *R. sumatrensis* by many internal anatomical characters.

PROVISIONAL GROUPING OF THE RHINOCEROTIDÆ.

ACERATHERIINÆ.	DICERATHERIINÆ.	CERATORHINÆ.	ELASMOTHERIINÆ.
All primitive and some specialized Rhinoceroses. Nasals and frontals with horns absent or rudimentary.	Specialized. Nasals with a pair of lateral horns.	Specialized. Nasals enlarged with median horns. Frontals with or without horns.	Specialized. Nasals reduced, without horns. Frontals with median horns.
Digits 4-3 : 3.	Digits 3 : 3.	Digits 3 : 3.	Digits 3 : 3.
<i>Dolichocephalic.</i>	<i>Dolichocephalic.</i>	<i>Dolichocephalic.</i>	<i>Dolichocephalic.</i>
Including all Oligocene Aceratheres, and the Upper Miocene <i>A. incisivum</i> .	Including the single Lower Miocene genus <i>Diceratherium</i> .	Including all known Pliocene and Pleistocene Rhinoceroses of Europe, excepting <i>R. pachygnathus</i> .	Including the single Pleistocene genus, <i>Elasmotherium</i> .
<i>Brachycephalic.</i>		<i>Brachycephalic.</i>	
Including <i>Teleoceras</i> and all known Miocene and Pliocene Aceratheres, excepting <i>A. incisivum</i> .		All known Miocene Rhinoceroses of Europe. Recent Rhinoceroses excepting <i>R. sumatrensis</i> .	

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NOTE.—Several of these References have not as yet been accessible to the author.

Part II.—ACERATHERES OF THE AMERICAN OLIGOCENE.

CRANIAL AND DENTAL CHARACTERS.

The remarkable series of Aceratheres from all levels of the American Oligocene obtained by the American Museum expeditions of 1892 and 1894 supplements our previous knowledge, and throws a flood of light upon the older Rhinoceroses of North America. Each of the main geological subdivisions of the Oligocene has one or two characteristic species which exhibit a sequence in progressive modernization, as shown in the thirty-five skulls, the numbers of which are presented in the geological table below. In such an abundant and evenly-distributed series, through successive levels, the usual sharp lines of specific demarcation are obliterated by transition forms, and certain nodal points of development must be taken for specific definition.

The geological distribution of these species begins with the Lower Oligocene, or Middle and Upper Titanotherium Beds, and, so far as we know at present there are probably two phyletic lines at least from this point to the top of the Oligocene, as indicated by differences in the shape of the lower canines (see p. 115), and the typical or atypical mode of metamorphosis of the superior premolars (see p. 114).

This division into two series must be accepted with some reserve. The two modes of premolar metamorphosis, and the two types of canines characteristic of these two series are probably but not certainly distinctive; it is

SERIES I.	SERIES II.
<p>In which the postero-internal cusp of the superior premolars is mainly attached to the incipient posterior crest. Lower canines oval in section, procumbent. Occiput progressively low and broad.</p> <p>This series appears to be ancestral to the Miocene Aceratheres.</p> <p><i>Aceratherium hesperium</i> Leidy.¹ <i>Aceratherium mite</i> Cope. <i>Aceratherium simplicidens</i> Cope.¹ <i>Leptaceratherium trigonodum</i> O. & W. <i>Aceratherium platycephalum</i> O. & W.²</p>	<p>In which the postero-internal cusp of the superior premolars mainly arises from the anterior crest, and is secondarily united with the posterior crest. Lower canines triangular in section, oblique. Occiput progressively high and narrow.</p> <p>This series appears to give rise to the Miocene Diceratheres.</p> <p><i>Aceratherium copei</i> Osborn. <i>Aceratherium occidentale</i> Leidy. <i>Aceratherium tridactylum</i> Osborn.</p>

¹ *Incertæ sedis.*

² This animal is not a successor of the preceding species.

not absolutely demonstrated that there may not be some elements of individual variability in this character. We seem to be at or near the parting of the ways between two phyla, and the final demonstration of this fact will probably be afforded by the skeleton.

SERIES I.

The first series is less fully known than the second, and we have as yet no certain knowledge of the foot-structure, as to whether there were four digits or three in the manus. It embraces the very large animal, *A. platycephalum*, possibly identical with *A. hesperium* Leidy, or *A. simplicidens* Cope, which persists in a nearly unmodified form from the Lower to the Upper Oligocene Beds, increasing very slowly in size, but not as yet recorded from the intermediate Oreodon Beds. The other species is *Leptaceratherium trigonodum*, known from the Lower Oligocene and Upper Titanotherium Beds of South Dakota, also from the Oreodon Beds, and well distinguished by the presence of a superior canine and by the simple triangular condition of the superior premolars, as the most primitive type of American Rhinoceros known. In the Titanotherium Beds of Colorado were also found by Cope the remains of the third species, *Aceratherium mite*.

The animals in this series are not known to succeed each other. On the other hand they appear to have existed contemporaneously in the Lower Oligocene.

Aceratherium mite was an extremely small animal, the femur and tibia together measuring only twenty inches (510 mm.), while the height of the body at the shoulder is estimated at twenty-eight inches (700 mm.). This was an animal, therefore, somewhat heavier in build, but not exceeding in dimensions the *Hyrachyus agrarius* of Leidy. The remains of several parts of the skeleton are known, but the complete structure of the skull is still unknown. This animal (Nos. 6325-6) was recorded from the Titanotherium Beds of Colorado by Cope, but the exact level was not ascertained. Of remarkable interest is the apparent existence of this diminutive species in the Upper Oligocene or Protoceras Beds.

Leptaceratherium trigonodum, judging by the size of the skull and teeth, was a somewhat larger animal, but no remains of the skeleton are known. It occurs in the top of the Titanotherium Beds, and, unlike *A. mite* and *A. platycephalum*, extends only into the Lower Oreodon Beds (Nos. 1131, 1138, 528, 529, 523). Its dental characters are much less modernized than those of either *A. mite* or *A. platycephalum*, but it does not appear to be ancestral to either. Its nearest general resemblances are with *A. copei*, and if the premolar metamorphosis is not found to be distinctive it may prove to represent an ancestor of that form.

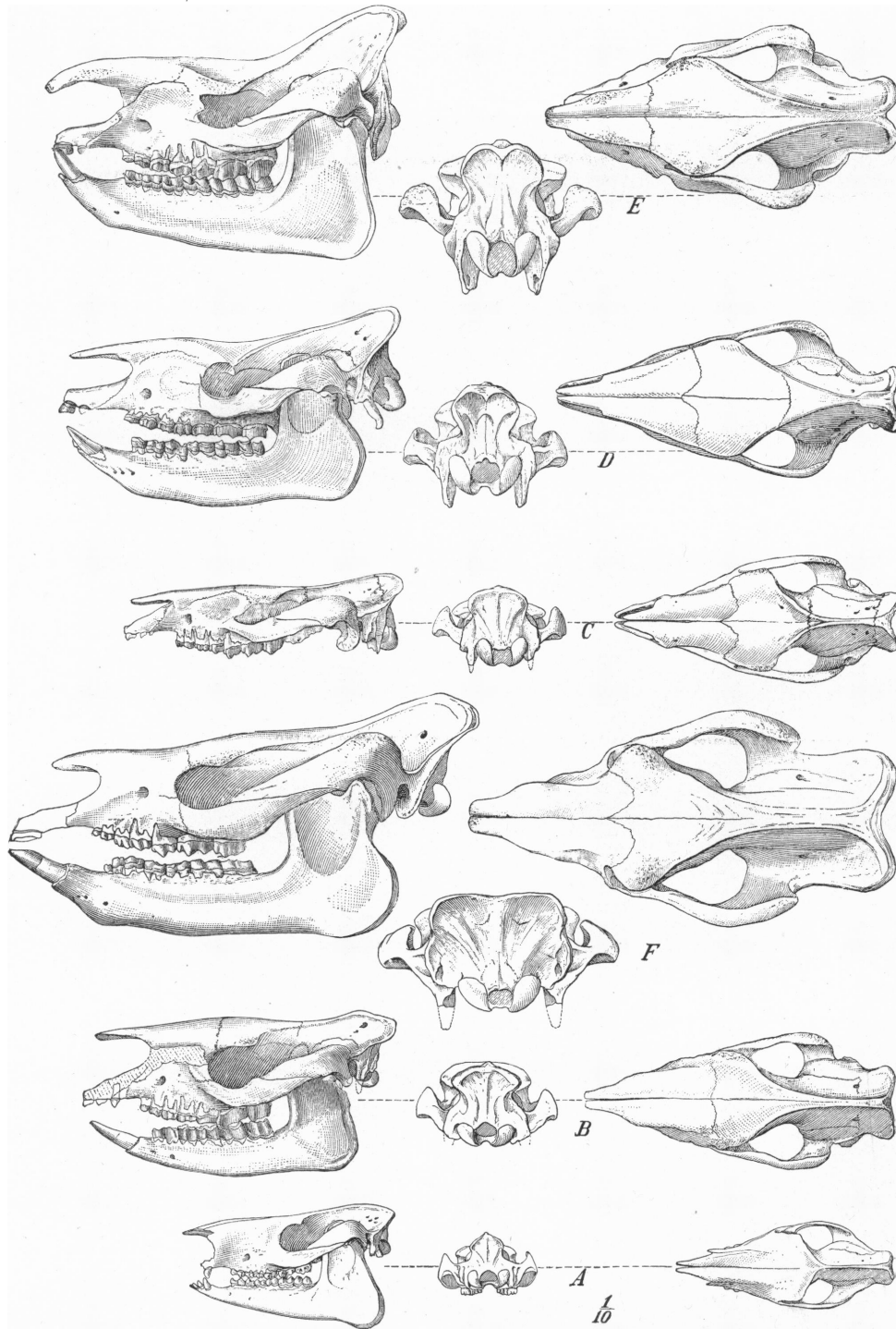


Figure 33. Showing successive stages in the Development of the Skull: *A*, *Hyrachyus agrarius* (No. 1645). Series I. *B*, *Leptaceratherium trigonodum* (No. 529); *F*, *Aceratherium platycephalum* (No. 1444). Series II. *C*, *Aceratherium copei* (No. 521); *D*, *Aceratherium occidentale*, composition; *E*, *Aceratherium tridactylum* (No. 538). From the Collection of the American Museum of Natural History.

Modified from HATCHER (1893, p. 204), WORTMAN (1893, p. 98), and OSBORN (1896, p. 197).

Modified from HATCHER (1893, p. 204), WORTMAN (1893, p. 98), and OSBORN (1896, p. 197).

[illegible]

¹ The exact level of these species in the Titanotherium Beds is not determined. The numbers are catalogue numbers of identified specimens in the American Museum Collection.

Aceratherium platycephalum is, on the other hand, an animal larger than the modern *Rhinoceros sumatrensis*, with heavy procumbent lower canines and low, flat occiput, no sagittal crest, and stout elongate metapodials. The nasals are short. There seems to be very little doubt that Mr. J. W. Gidley, in 1896, truly determined its occurrence in the Titanotherium Beds (No. 1478). The discovery of this animal in these beds of the Lower Oligocene was most surprising, and completely upset conclusions which we had formed previously as to the small size of the Lower Oligocene Rhinoceroses, and their lack of specialization, for here is a highly specialized animal, without upper canines, with lower canines of enormous size, overshadowing its contemporaries. It persists comparatively unmodified throughout the Oligocene, for it is found with substantially identical characters in the Upper Oligocene Protoceras Beds, where it was first discovered (Nos. 540, 542, 545, 1144) by the American Museum party in 1892.

SYNOPSIS OF PARALLEL AND DIVERGENT SPECIFIC CHARACTERS.

PARALLEL STAGES OF EVOLUTION.	FIRST SERIES.	SECOND SERIES.
	Lower canines, suboval, procumbent. Upper premolars with tetartocone connected mainly with metaloph. Number of digits unknown. Nasals progressively abbreviated.	Lower canines, subtriangular, oblique. Upper premolars with tetartocone primitively connected with protoloph. Digits 3-3. Nasals progressively elongated.
I. <i>Superior Canine persistent in Adult.</i> P ³ and p ⁴ with rudimentary tetartocone..	Genus LEPTACERATHERIUM. <i>L. trigonodum</i>	Undiscovered stage.
II. <i>Superior Canine temporary in Adult.</i> P ³ and p ⁴ with strong tetartocone.....	Genus ACERATHERIUM. <i>A. mite</i>	<i>A. copei</i> .
III. <i>Superior Canine absent in Young and Adult.</i> P ³ and p ⁴ with tetartocone joining metaloph.....	<i>A. platycephalum</i> .	
Pm ² and pm ³ molariform.	<i>A. occidentale</i> .
Pm ² , pm ³ and pm ⁴ molariform	<i>A. tridactylum</i> .

SERIES II.

The *second* series is closely connected and successive from *A. copei* in the base of the Oreodon Beds, through *Aceratherium occidentale* in the Middle Oreodon Beds into *Aceratherium tridactylum* in the Protoceras Beds, as

exhibited in the Stratigraphic Table. So far as known all these animals possessed but three digits in the manus, the fifth digit being vestigial. The three following species were undoubtedly successive :

Aceratherium copei, the oldest of this series, is first found at the very base of the Oreodon Beds, as represented by two skulls (Nos. 521, 522), in one of which the upper canines are temporarily retained. The lower jaws unfortunately are not known. These skulls present marked resemblances to that of *Hyrachyus agrarius*. The nasals are long and pointed. The limbs show only three digits in the manus. By a beautiful series of transitions this species passes through the Lower, Middle and Upper Oreodon Beds, into *Aceratherium occidentale*, the first Rhinoceros discovered in the Oligocene by Leidy.

Aceratherium occidentale, the characteristic Middle Oligocene form, in turn gradually develops a number of transformations in its premolar teeth, which might almost be assigned a specific value, in its passage into *Aceratherium tridactylum*, a type extremely abundant, and highly characteristic of the Protoceras Beds. Whereas *Aceratherium copei* is an animal about the size of the American Tapir, *Aceratherium tridactylum*, the skeleton of which has been described and figured by the writer, nearly equals the Sumatran Rhinoceros in size. The skeleton shown in Plate XX measures seven feet nine inches in length, and four feet in height, to the top of the lumbar vertebral spines. The total length of the skull is 510 mm., while in *A. occidentale*

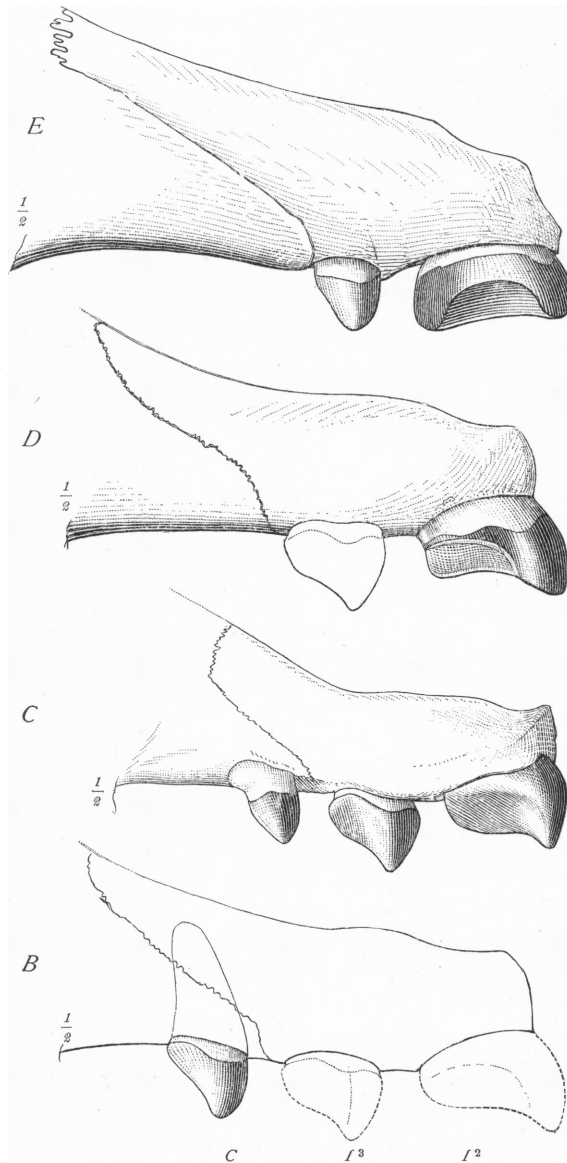


Figure 34. Premaxillaries and superior cutting teeth of American Oligocene Aceratheres, showing degeneration of superior canines and lateral incisors. *B*, *Leptacetherium trigonodum* (No. 529), partly restored. *C*, *Aceratherium copei* (No. 521), showing adult cutting teeth recently obtruded, including the temporary canine. *D*, *Aceratherium occidentale* (No. 1108), showing large size of lateral incisor. *E*, *Aceratherium tridactylum* (No. 538), showing reduced size of lateral incisor. In the collection of the American Museum of Natural History.

it measures 440 mm. Another progressive feature is that the molar teeth show the beginning of a crochet, which is wholly undeveloped in *A. occidentale*. As above noted, *Aceratherium platycephalum* is a contemporary of this animal, but is of very much larger size.

It will be interesting to trace the ultimate development of these two series in the Miocene, when the John Day types become better known. It is possible that the first series may be characterized by persistent fifth digits and shortened nasals, and thus parallel the four-toed *Aceratheres*, such as *A. tetradactylum* of Europe. The second appears to give off the *Diceratheriinae* of the Lower Miocene.

It is obvious that *Aceratheres* with persistent upper canines are distinct from *Aceratheres* with temporary or no upper canines, and to the former the new generic name *Leptaceratherium* may hereafter be applied.

Leptaceratherium, gen. nov.

Ancestral Rhinoceroses with sub-functional superior canine teeth. Two pair of upper incisors; one pair of lower incisors.

Leptaceratherium trigonodum (O. & W.).¹

PLATE XII; PLATE XIII, Fig. 1; PLATE XIX, Fig. 27.

Specific Characters.—Dentition, I_1^1 , C_1^1 , Pm_3^3 , M_3^3 . (a) Upper canine apparently persistent in the adult and well developed; lower canine large, suboval, and procumbent. (b) Second upper premolar with metaloph consisting of a short crest united with a tetartocone. Upper premolars 3 and 4 subtriangular with tetartocone rudimentary or absent; third premolar with tetartocone rudimentary or absent; if present, developed towards the base, and chiefly connected with metaloph; fourth premolar with a single internal lobe, a feeble or incipient postero-internal spur (tetartocone) connected with the metaloph, and a somewhat prominent elevation of the postero-internal cingulum, which presents the appearance of a 'cingule' when worn. (c) Upper molars with or without internal cingulum upon protoloph; cingulum becoming apparent upon wear. (d) Skull (No. 529) fairly elevated; sagittal crest low, nearly obsolete; nasals rather short, not notched; postglenoid and posttympanic processes widely separated.

Type. Maxilla, No. 528; cotype, skull, No. 529. American Museum Collection.

Geological Level.—The type of this species was found in the Upper Titanotherium Beds. It consists of a fractured palate (No. 528) and double set of upper premolars and molars, lacking pm^1 . The cotype is a nearly perfect skull (No. 529) and lower jaws with the inferior median incisors and pm^1 missing; it was found in the Upper Titanotherium layer or extreme base of the Oreodon Beds.

A third nearly complete skull (No. 1131) was also found in the Titanotherium Beds of South Dakota; the teeth have substantially the same characters. The strictly triangular form of the fourth upper premolar is the basis of the specific name *trigonodum*, but the apparently persistent and well-developed canine is also a highly distinctive character.

¹ Bull. Am. Mus. Nat. Hist., Vol. VI, July, 1894, p. 202.

The species or stage may readily be distinguished by the absent or rudimentary postero-internal cusp of the third and fourth upper premolars, which mark it, with the canine, as the most primitive *Rhinoceros* known.

The postero-internal cusp, when it arises, springs from the metaloph. Thus the species is in the same class as *A. mite* and *A. platycephalum*.

Dentition.—The lower lateral canines and the upper canines are preserved in the fully adult skull, No. 529, but the premaxillaries and upper incisors are missing. The upper canine is a small, stout-fanged, short-crowned tooth, laterally compressed; it was not found *in situ*, but there is no doubt of its association with the skull, as it agrees closely in form with the more temporary canine of *A. mite*.

The lower canines are very distinctive in form and position, being almost completely procumbent, a rare feature in a primitive type (See Fig. 35). The incisor alveoli indicate that these teeth were also procumbent.

Premolars and Molars.—*Superior.* Beginning with the dentition of the type (No. 528), we observe that the *fourth premolar* has an absolutely single internal lobe or deutocone, embraced by a wide and deep cingulum; the second internal lobe or tetartocone is represented by a rudimentary spur upon the metaloph; the metaloph is a depressed delicate crest; the protoloph is prominent internally, but not recurved as in *Hyrachyus*, or in *A. copei*; the ectoloph is elevated, flattened and symmetrical, with three vertical ridges (parastyle, protocone and tritocone). The *third premolar* has a confluent but double internal cone at the close junction between the protoloph and metaloph; the tooth is slightly more quadrate than pm^4 . The *second premolar* has two completely separated internal cones with complete and approximately equal-sized protoloph and metaloph; the contour is fully quadrate; as in *A. mite*, the tetartocone unites with the metaloph. The *first premolar* is a small irregular tooth with an elongated ectoloph and a larger metaloph than protoloph. The true *molars* are characterized by a distinct cingulum around the protoloph; an antecrochet quite strongly developed in m^1 , less so in m^2 , and wanting in m^3 ; there are strong anterior and posterior cingula.

The superior dentition in the skull (No. 529) is slightly more modernized than in the type specimen, for there is a faint reduplication of the internal lobe of the fourth premolar. The skull is also of slightly larger size, as we should anticipate from the fact that it belongs upon a slightly higher level. As an important variation we observe that the protoloph in both the premolars and molars is devoid of the internal cingulum, which is a marked feature of the type. It is possible that these characters are specific; they appear, however, to represent a variation. The inferior cheek-teeth grinders of No. 529 are exceptional in including only *three* premolars, thus agreeing with *A. mite*. In the third and fourth lower premolars the

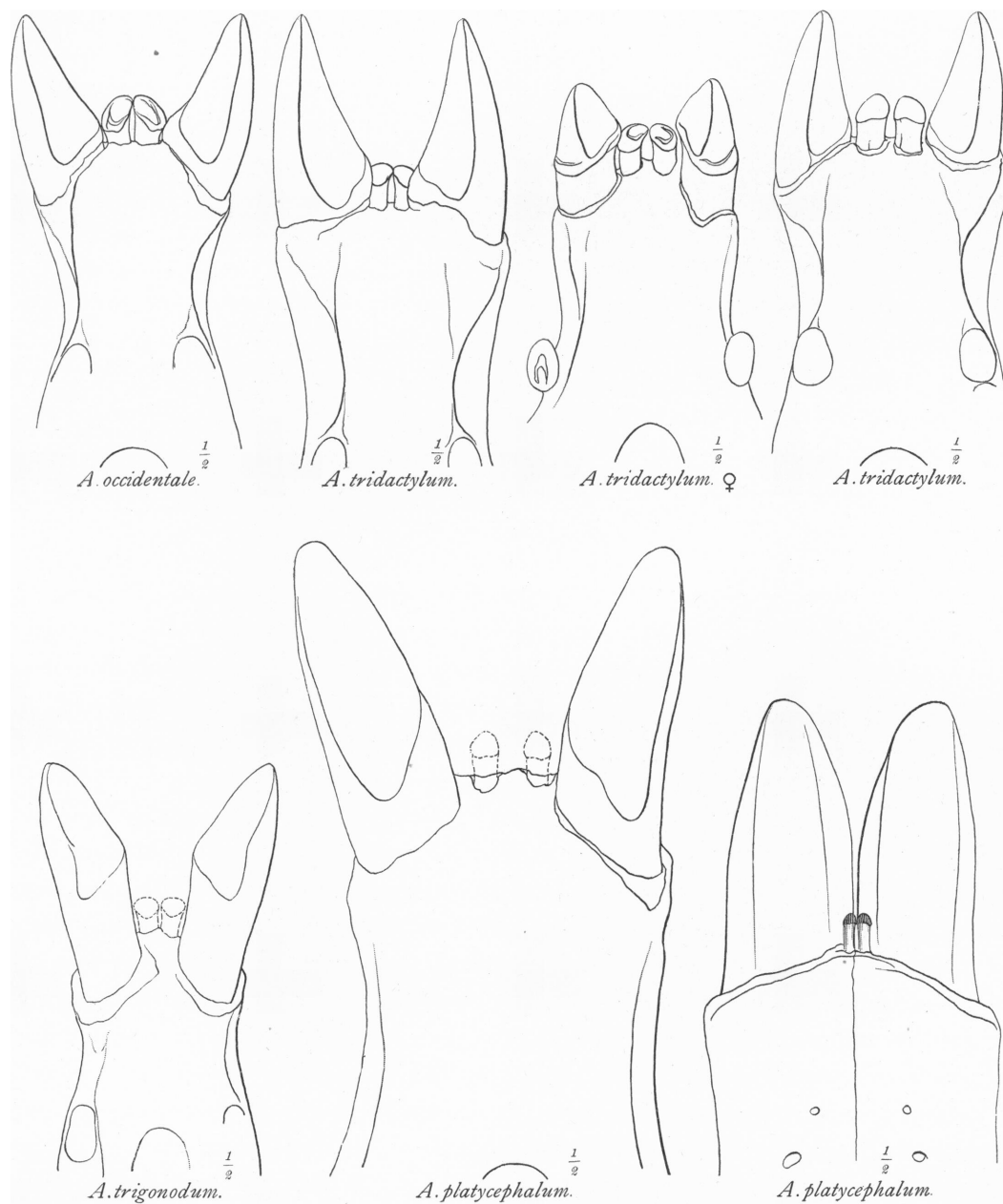


Figure 35. Mandibular Symphyses of American Oligocene Aceratheres, showing specific, sexual, and progressive characters of the inferior cutting teeth. Series I. Suboval procumbent, lower canines greatly enlarged, lower incisors rapidly reduced. Superior view of *L. trigonodum* (No. 529); superior and inferior views of two specimens of *A. platycephalum* (Nos. 545, and Princeton Mus.). Series II. With triangular lower canines and slow reduction of lower incisors, *A. occidentale* (No. 1144); *A. tridactylum*, adult male (No. 538); *A. tridactylum*, female (No. 543); *A. tridactylum*, young male.

metalophid is considerably stouter and heavier than the hypolophid. In the lower molars these crests are more nearly sub-equal; the metalophid is most worn. Neither premolars nor molars exhibit cingula.

MEASUREMENTS.

	No. 528.	No. 1131.	No. 529.
	MM.	MM.	MM.
Superior premolar-molar series	173	183	183
Inferior " " " "	165
Superior molars	100	100	100
Occiput to nasal tips	435
Transverse zygomatic arches	197	200
Occiput, height	107	113
" width	94	100

Skull.—The skull in general is rather long and narrow in proportion ; the cranium, taking the mid-orbit as a central point, is considerably longer than the face, the proportions being 240 to 200 mm. ; the superior profile is nearly a plane. There is a considerable extension of the cranium behind the zygomatic arches, which is a distinctively primitive feature. The total length is about 17 inches (435 mm.) ; the greatest breadth is $7\frac{1}{8}$ inches, or 198 mm.

In *lateral* view (Pl. XIV, Fig. 12), we observe the following features : The upper profile is plane ; the lachrymals appear to extend widely upon the face ; the lachrymal notch is at the upper corner of the orbit ; the infraorbital foramen is just above the second premolar ; the zygomatic arches are slender, rising slightly posteriorly ; there is a large single parietal foramen ; the auditory meatus is widely open inferiorly ; the occiput spreads superiorly and overhangs the condyles.

In *superior* view (Pl. XIV, Fig. 11) the skull exhibits smooth, rounded nasals which taper very gradually to the extremities and are not notched at the sides as in *Hyrachyus agrarius* or in *Aceratherium copei* ; the naso-frontal suture is directly above the front border of the orbit ; the frontals extend back to the narrowest point of the cranium just in front of the brain-case ; the space between the supraorbital processes of the frontals is moderately broad ; the supraorbital rugosities are very slight ; the faint superciliary or sagittal ridges converge gradually into the sagittal crest, which is remarkably low or sessile for so ancient a type ; it is only clearly constricted off in the posterior third of the brain-case ; the superior border of the occiput is heavy and deeply notched ; the zygomatic arches are slender, they diverge slightly posteriorly and are connected with the skull by a rather narrow, horizontal squamosal plate ; behind this the skull is considerably elongated. The occiput (Pl. XIX, Fig. 2) is rather lower and broader in its proportions than in *A. copei*, the supraoccipital crest extends somewhat more widely above, although these differences are not very decidedly marked. Below the superior border the posterior surface is deeply hollowed ; seen from this point, the zygomatic arches are slender and the occipital condyles small.

In the *inferior* view of this skull (Pl. XIV, Fig. 13) we observe that the palate is slightly fractured ; the posterior nares are widely open ; the

postglenoid process is relatively broad, obliquely placed *behind* rather than internal to the glenoid fossa as in *A. copei* and later types; it is slightly antero-verted; just internal to this process is the opening of the foramen ovale, widely separated from the foramen lacerum medium; at the antero-internal angle of the glenoid fossa is the alisphenoid canal; the basi-sphenoid is rounded, while the basi-occipital has a depressed median keel; the large periotic mass lies deeply imbedded upon either side of this basi-cranial axis between the foramen lacerum medium and foramen lacerum posterius; the pterygoids are of moderate length.

Foramina.—The alisphenoid canal, the f. ovale, f. lacerum anterius, f. lacerum posterius and f. condylare are small, distinct and linearly arranged. The space between the f. ovale and f. lacerum medius measures 130 mm.

The *lower jaws* of No. 529 (Pl. XIV, Fig. 12) exhibit slender rami, shallow at the chin, a short symphysis and short diastema between the canines and second premolars. The coronoid is slender; the condyle faces upwards and backwards; behind this is an incipient cotyloid process; the angle is perpendicular to the lower border of the jaw. There are four mental foramina.

Aceratherium Kaup.

Hornless Rhinoceroses with superior canines temporarily developed or wanting. Superior incisors 2-1. Inferior incisors 1-0. Digits of the manus 4-3:3.

SYN.—*Ronzotherium* AYMARD, (1854); *Aphelops* COPE (1873) [in part]; *Peraceras* COPE (1880); *Canopus* COPE (1880).

Mention has already been made (p. 119) of the difficulty of adopting any consistent rule in regard to the generic divisions of the Rhinoceroses. Subsequently, when the skeletal characters are more thoroughly known, and especially the foot structure, we may be able to separate these species by definitions which will hold good in all cases.

Aceratherium mite Cope.

SYN.—*Aceratherium* (*Canopus*) *pumilum* COPE (1885, 1, 2).

Specific Characters.—Dentition, I_1^2 , C_1^{1-0} , Pm_4^{1-3} , M_3^2 . Diastema short. Lower canines small, alveoli semi-procumbent. Premolar-molar series $\frac{1}{4}\frac{1}{2}$ mm. Mandibular symphysis very short. Second and third superior incisors large. Superior canine shed in adult. First upper premolar reduced. Third and fourth upper premolars subtriangular, tetartocone spur connected with metaloph. Internal cingulum very faint. Antecrochet rudimentary upon m^4 .

Type.—Lower jaw without teeth, No. 6325, Am. Mus., Cope Coll. Cotype: Maxilla with teeth, fragmentary skull and portions of skeleton, No. 6525, Am. Mus., Cope Coll.

Geological Level.—This, as the name indicates, is the smallest known American Acerathere. The type geological level is the Titanotherium Beds of Colorado. It has also been found (*A. pumilum*) in the Swift Current Creek exposures of British Columbia. Although we cannot speak positively,

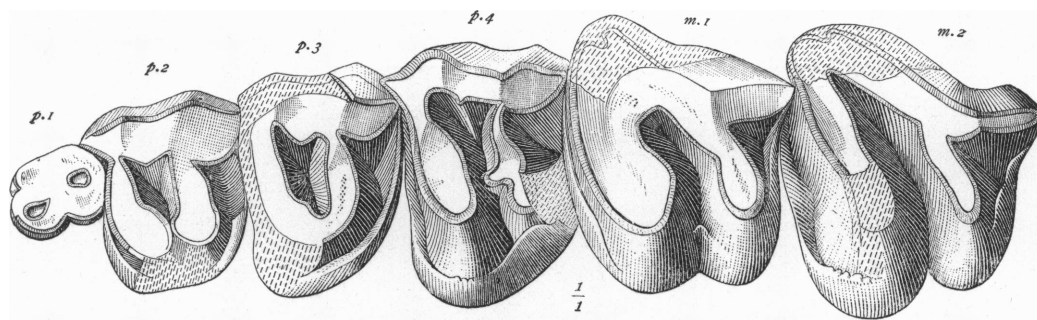


Figure 36. *Aceratherium mite* Cope. Cotype specimen probably belonging with type of lower jaw, showing atypical mode of metamorphosis of fourth superior premolar; tetartocone rising from metaloph and not connected with metaloph. Collection American Museum of Natural History, No. 6325.

it is probably one of the oldest of the Aceratheres, but not as primitive in the structure of its grinding teeth as *L. trigonodum*, because it has a well-developed tetartocone upon the fourth upper premolar. It is certainly characteristic of the Titanotherium Beds or Lower Oligocene. It is a smaller animal than *L. trigonodum*, but the teeth are somewhat more modern in type, especially in the absence of upper canines and the modifications of the premolars.

HISTORICAL NOTES.

The animal was discovered by Cope himself in the Symborodon or Titanotherium Beds of northwestern Colorado in 1873, apparently represented by the remains of two individuals lying near together. In his original type description¹ Cope (1875, p. 493) first mentioned a very uncharacteristic and fragmentary lower jaw, which must be taken as the type. Found near this jaw were vertebræ

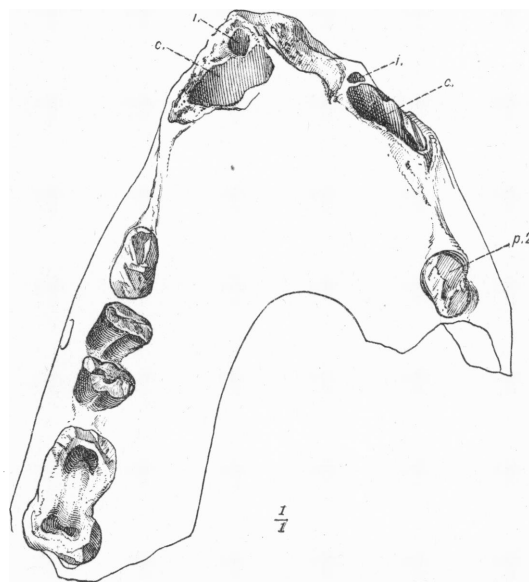


Figure 37. View of symphysis of cotype specimen of *Aceratherium (pumilum)* Cope. Collection of the Canadian Geological Survey, Ottawa. (Cast 10,386, Am. Mus. Collection.)

¹ Ann. Rep. U. S. Geol. Surv. Terr., 1873 (1874), p. 493.

and limb-bones supposed to belong to the same individual, besides maxillary teeth and skull fragments from the same or other individuals.

In 1885 Cope received two jaw-fragments from the Canadian Geological Survey, which had been discovered in the Swift Current Creek, Oligocene of British Columbia. He named them¹ *Aceratherium* (*Cænopus*) *pumilum*, selecting as a type the anterior portion of a jaw (Fig. 38) containing two deciduous premolars and one molar, this fragment certainly being not an Acerathere at all, but an Hyracodon. The second or cotype (Fig. 37) is

however an Acerathere symphysis, without teeth, and may be taken hereafter as the type, since it embraces one of the principal characters Cope assigned to the species, namely the small procumbent lower canines. The measurements of the symphysis of the cotype are nearly identical with those of the type jaw of *A. mite*, namely: antero-posterior diameter, 38 mm.; vertical diameter, 22 mm. There is a

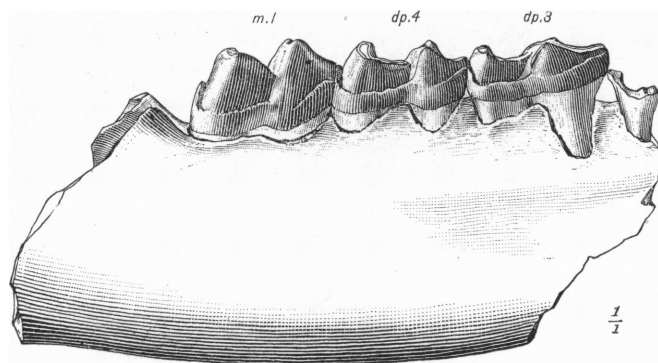


Figure 38. Side view of the type of *Aceratherium pumilum* Cope, a young jaw of *Hyracodon nebrascense*. Collection of the Canadian Geological Survey. (Cast 10,386, Am. Mus. Coll.)

vestigial pm_1 ; the spaces for the three functional premolars measure only 43 mm., somewhat less than the three *A. mite* premolars. Other characters, such as the position of the mental foramen, the depth of the rami, etc., correspond so closely that there is no doubt we have here a lower jaw in the *A. mite* stage of development.

Fortunately the American Museum Expedition of 1892 secured in South Dakota a perfect lower jaw (No. 1110) which agrees exactly with the above specimens, enabling us to clearly distinguish this diminutive animal. It was found, according to the field notes, in the Protoceras Beds, or Upper Oligocene, but its characters agree closely with those of *A. mite*.

CRANIAL AND DENTAL CHARACTERS.

It is important to separate the features derived from the lower and upper jaws which Cope selected as types, for there is some doubt as to their association. They are as follows:

¹ Amer. Nat., 1885, p. 103 (name only). Ann. Rep. Geol. & Nat. Hist. Survey of Can., 1885, Appendix C, p. 83.

Characters of Type Jaw.—Dentition C_1 , Pm_3 , M_3 . Diastema short. Canine alveoli semi-procumbent. Premolar-molar series 142 mm. Mandibular symphysis very short. Locality, Colorado. Am. Mus., Cope Coll. No. 6325.

Characters of Cotype, Maxilla.—Canine shed in adult. First upper premolar reduced. Third upper premolar with confluent internal crests. Fourth upper premolar subtriangular with distinct posterior crest consisting of tetartocone confluent with metaloph. Molars with faint internal cingulum upon protoloph; metaloph smooth. Antecrochet developed in m^1 , and less strongly in succeeding teeth. Premolar-molar series estimated 160 mm.

Cope's Original and Cotypes.—The type lower jaw (No. 6325) is slender and tapers towards the symphysis, which is extremely short. The antero-posterior measurement of the symphysis is 40 mm.; the vertical measurement is 19 mm. Only the roots of the lower canines are preserved, and they are close together, indicating that these teeth were very small and procumbent. The fractured crowns of three premolars preserved upon the left side measure 55 mm.; while the fractured molar crowns preserved on the right side measure 87 mm. Thus the total molar-premolar measurement is estimated at 142 mm. The depth of the jaw below the last molar is 52 mm.

Cutting Teeth.—The lower canines in the type were evidently small, semi-procumbent, and close together. The fang measurement is 9.9 mm. x 9 mm. The incisor alveoli are worn away. The associated premaxillary bone (No. 6325) shows a lateral incisor (i^3) alveolus, measuring 16 x 11 mm.

as compared with 12 x 9 mm. in Skull No. 522. This indicates that in *A. mite* the third incisor was as large as the second, whereas in *A. copei* the third incisor is considerably smaller than the second. The growth of the second incisor at the expense of the third is a marked feature of the ascending series.

Grinding Teeth.—The associated upper maxillary series (No. 6325) measures, premolars 98 mm., and the molars are estimated at 87 mm., giving a total estimated measurement of 155. The first upper premolar is reduced, corresponding with the reduced or degenerate condition of the first lower premolar. The second has two distinct internal crests. In the third the internal

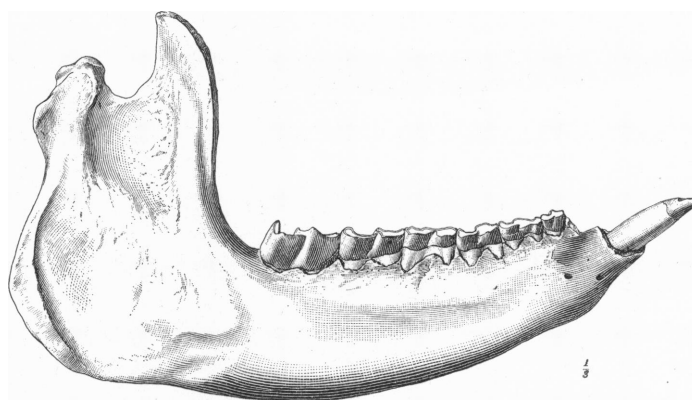


Figure 39. Lateral view of small lower jaw (No. 1110), from the Protoceras Beds, doubtfully referred to *Aceratherium mite* Cope. Collection of the American Museum of Natural History.

crests are confluent in the worn condition. In the associated maxillary (No. 6326) both the second and third premolars show the tetartocone as a distinct element, uniting with the metaloph, this being the distinctive feature of this species. The fourth premolar is triangular in form but exhibits a distinct protoloph and a metaloph which sends forwards a vestigial inner spur of union while externally it unites directly with the tetartocone. This, as already remarked, is sharply different from the structure of the metaloph in *A. copei*, as seen in the American Museum skulls Nos. 522 and 521. The antero-posterior measurement of the first molar is 27 mm. The cingulum is not very clearly defined upon the protoloph, but this tooth agrees exactly in measurement with the first molar in skull No. 522.

The fine jaw (No. 1110) discovered in the Protoceras Beds (Fig. 34) cannot be specifically distinguished from Cope's types of *A. mite* or of *A. pumilum*, although occurring in a very much more recent level. The length of the jaw from the angle to the symphysis is only 10 inches (255 mm.); the length of the six molar-premolar teeth is 124 mm., and that of the true molars is 77 mm. The depth of the ramus below the third molar is 54 mm. The border of the angle is rugose. There is a sharp inturned postcotyloid process. The condyle is extremely convex antero-posteriorly, and widely extended antero-posteriorly. This seems to afford positive proof of the existence of a very small species of *Aceratherium* during the deposition of the Protoceras Beds, but whether or not it represents a persistence of the *A. mite* type depends upon the structure of the upper teeth, which are unknown.

Aceratherium platycephalum O. & W.

PLATE XIII, FIG. 9; PLATE XVIII.

Specific Characters.—Dentition, I_1^2 , C_1^0 , Pm_{3-4}^4 , M_3^3 . (a) Lateral upper incisors reduced; lower incisors greatly reduced. (b) Upper canines wanting in permanent series; lower canines greatly enlarged, with procumbent, suboval crowns. (c) Third and fourth upper premolars with slender metaloph and separate tetartocone, when unworn; protoloph large. (d) 'Antecrochet' upon first and second upper molars; vestige of postsinus in third upper molar. (e) Skull broad and low; occiput quadrate; sagittal crest sessile, nearly obsolete; postglenoid and posttympanic processes in limited contact; nasals short.

Type.—A skull nearly complete but vertically crushed (No. 542, Am. Mus. Coll.), with teeth well worn. *Cotype*.—A right maxilla with all the grinding teeth unworn (No. 540, Am. Mus. Coll.).

This species was established by Osborn and Wortman in 1894 upon the very characteristic flattened cranium (No. 542) which suggested the name. The cotype is the molar series figured in Plate XIII. Other characters were derived from a fine lower jaw (Am. Mus. Coll., No. 1444) lacking only pm_{1-2}

and the incisors ; also from a second jaw (Am. Mus. Coll., No. 545) lacking the ramus behind the last molar. The characters observed in these specimens were confirmed and added to by the discovery of a complete skull and jaws which, although laterally crushed, fortunately contains the second upper incisors, and is now preserved in the Princeton Museum. All the above materials were secured in the Upper Oligocene Protoceras Beds of South Dakota, and it was assumed that *A. platycephalum* was an Upper Oligocene type. In 1896, however, a fine skull and jaws were found by Mr. Gidley in the Titanotherium Beds or Lower Oligocene levels of the

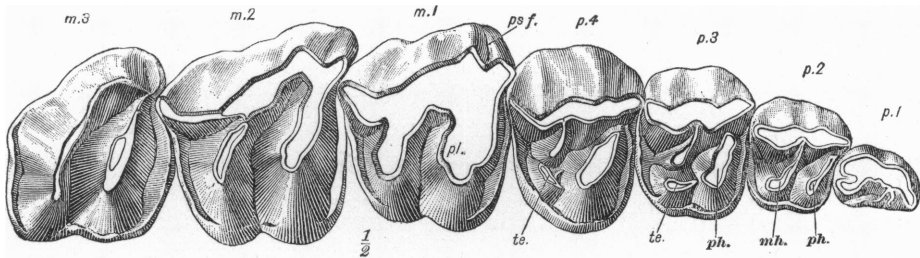


Figure 40. Superior premolar-molar series of type specimen of *Aceratherium platycephalum*, showing atypical evolution of tetartocone, midway between protoloph and metaloph. Collection of the American Museum of Natural History, No. 540.

Hat Creek Basin exposures, Nebraska. This skull is throughout a shade smaller, but agrees very closely in all its characters with the others, and undoubtedly belongs to the same species. It closely resembles the type of *A. hesperium* (Leidy).

This animal is readily distinguished by its very large size ; its broad low occiput ; flattened and crestless cranium ; orbits anteriorly placed ; short obtuse nasals ; very large and procumbent lower canines. The skull (No. 1478) from the Titanotherium Beds is half as long again as that of the contemporary *A. mite*, the linear measurements along the axial line being in the ratio of 590 mm. to 405 mm.

MEASUREMENTS OF AMERICAN MUSEUM SPECIMENS.

	Type. No. 540.	Cotype. No. 542.	Jaw. No. 545.	Jaw. No. 1444.	Skull. No. 1478.
	MM.	MM.	MM.	MM.	MM.
Superior molar-premolar series.....	238	236	227
“ molars 	133	139	128
Inferior molar-premolar series.....	228	222	213
“ molars 	135	142	133
Skull, premaxillaries to condyles.....	590
“ width of zygomata.....	? 360	294
Jaws, angle to point of symphysis.....	530	501

DENTITION.

PLATE XIII, FIGS. 9 AND 10.

Upper Grinding Teeth.—The first upper premolar in the type (No. 540) is an elongate laterally compressed tooth with two internal spurs representing the transverse crests. The second upper premolar is broad with vertical external 'costæ' and two complete internal crests. The third premolar is quadrate but not molariform; the protoloph has a sharply-defined and somewhat separate tetartocone; the metaloph is a short demi-crest, quite distinct from the tetartocone, even when well worn (see Fig. 10). The fourth premolar is subtriangular, with the tetartocone less strongly developed, and in the unworn condition quite distinct from the prominent protoloph and short, sharp metaloph. The true molars lack internal cingula, but have sharply-defined anterior and posterior cingula, and a prominent median 'costa' or paracone; the protoloph in the first and second molars has a strong 'antecrochet.' In the third molar the vestige of the postsinus or primitive valley, between the ectoloph and posterior surface of the metaloph, is represented by a shallow pit, more pronounced than in *A. tridactylum* or *A. occidentale*, and resembling that in Cope's *A. simplicidens*.

The characters of the premolar teeth in the cotype (No. 542) are similar, except that the greater wear has united the metaloph and tetartocone into a single crest (Plate XIII, Fig. 10). In the Lower Oligocene specimen (No. 1478) the tetartocone is united by wear with the protoloph.

Lower Grinding Teeth.—The first lower premolar is a small and variable tooth. In two jaws (Nos. 545, 1478) it is present in one ramus and absent in the other. The remaining premolars 2-4 in all the specimens (Nos. 545, 1444, 1478) are distinguished by the very imperfect development of the posterior crests, a condition correlated with the retarded development of the posterior crests in the superior premolars. As in the upper jaw the true molars are large and strongly developed.

Cutting Teeth.—The very powerful and procumbent lower canines (see Fig. 35), deeply implanted in the long symphyseal portion of the ramus, and the small degenerate pair of lower incisors, form a very distinctive feature of this species. In section the canines resemble those of *A. incisivum* (Eppelsheim) and *A. tetradactylum* (Sansan), as figured by Mermier (1895, p. 30, Figs. 6 and 7). The median upper incisors are not known, but were undoubtedly very large also. The outer pair of upper incisors are reduced and appear to be variable; they are present in the Princeton Museum specimen, but are absent in our geologically older specimen from the Titanotherium Beds (No. 1478).

CHARACTERS OF THE SKULL.

In the lateral view of the skull we are struck by the anterior position of the orbit due to the elongation of the cranium posteriorly. The premaxillaries are widely separated from the nasals, whereas in *A. mite* they are nearly if not quite in contact. There is a wide space between the orbits and the narial notch, and the free portion of the nasals is correspondingly short. The shortening of the nasals is exaggerated in Plate XIII, and is more correctly represented in Fig. 41. There is a very prominent and characteristic rugose swelling above the orbits. The superior profile of the mid-cranium is decidedly depressed, owing to the obsolete condition of the sagittal crest. The postglenoid and posttympanic processes are in contact even in the skull from the lower or Titanotherium Beds. The occiput slightly overhangs the condyle.

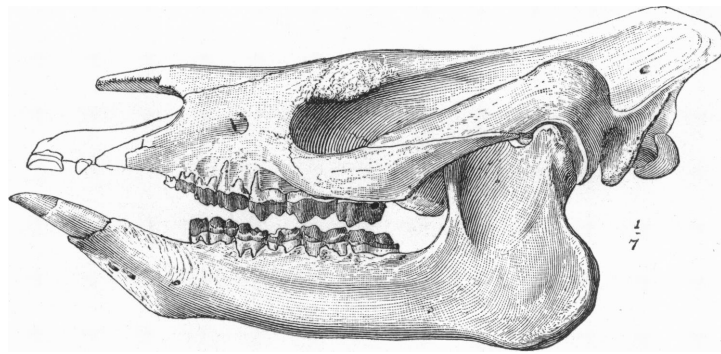


Figure 41. *Aceratherium platycephalum*. Side view of skull. The contour of the anterior portion of the skull and jaws is more accurately represented here than in Plate XVII. Collection of the American Museum of Natural History (Nos. 542, 1444).

In superior view we are struck by the backward extension of the naso-frontal suture into the prominent bosses above the orbits. The frontals are short. The sagittal crest is practically obsolete, the supraorbital line being carried back to the occipital crest. The zygomatic arches do not spread suddenly as in *A. tridactylum*, but arch gradually outwards.

The occipital view (Plate XX, Fig. 31) is highly characteristic, the superior line of the crest being very broad and horizontal, as in the Upper Miocene types, instead of being laterally compressed as in all the other species. In the basal view of the skull (No. 1478) the premaxillaries are widely separate in the median line. The molar series are nearly parallel; the posterior nares open in front of the third molar. The pterygoids are short. The f. ovale is separated by a distinct bridge of bone from the f. lacerum medium. The postglenoid process is internal in position, and has a narrow contact with the posttympanic, closing in the auditory meatus inferiorly. The paroccipital process is a flat, obliquely-placed plate. The periotic mass is small and depressed.

Aceratherium (Rhinoceros) hesperium Leidy.¹

Specific Characters.—Dentition, I_T , C_T , Pm_T , M_T . Lower canine large and procumbent. Lower premolar series relatively reduced.

Type.—A right mandibular ramus in the Collection of the Geological Survey of California.

The important type jaw of this species was sent to Dr. Leidy in 1865 by Prof. J. D. Whitney of the Geological Survey of California. It was found in Chili Gulch, Calaveras Co., California, in a matrix closely resembling that of the White River, Dakota. It consists of a right ramus, containing three

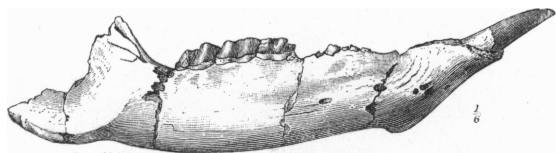


Figure 42. Lateral view of type lower jaw of *Rhinoceros hesperius* Leidy. After Leidy (1869). In the Collection of California Geological Survey.

molars, the fangs of four premolars, the canine, and alveoli of the median incisors. The accompanying figure is taken from Leidy's plate (*op. cit.*, Pl. XXIII). The writer has been unable to examine the type.

It is described by Leidy as follows: The jaw is deeper below the molars than in *A. occidentale*;

the chin is more robust, in keeping with the more powerful lower canines. The symphysis is 52 lines (132 mm.) in length, and 29 lines (74 mm.) in breadth. The diastema is $2\frac{1}{2}$ inches, and has a prominent acute edge.

The grinding teeth are reduced anteriorly, the premolars being proportionally smaller than the molars as compared with *A. occidentale*; the whole series measures 78 lines (198 mm.), while the premolars measure 30 lines (76 mm.). It is an important point that in *A. occidentale* the premolars occupy about an inch less space than the molars, whereas in *A. hesperium* they occupy $1\frac{1}{2}$ inches less. The crown of the canine is worn off internally in a long triangular slope; it measures $1\frac{1}{2}$ inches in length. The measurements are summarized as follows:

	<i>A. hesperium.</i>	<i>A. platycephalum.</i>
	MM.	MM.
M^3 to incisive alveoli inclusive.....	335	313
Depth of ramus, below m^3	87	91
“ “ below pm^2	76	57
“ symphysis.....	132	..
Length of “.....	..	122
M^3 to pm^2 , inclusive.....	198	205
True molar series.....	121	132
Pm^2 – pm^4 , inclusive.....	76	83
Length of diastema.....	76	70

¹ Proc. Acad. Nat. Sci. Phil., 1865, p. 176. Also 'On the Extinct Mammalia of Dakota and Nebraska,' 1869, p. 230.

This animal agrees very nearly in several characters with the smaller type of *A. platycephalum* found in the Titanotherium Beds (No. 1478), especially in the lower diastema, the relatively reduced premolars, the procumbent position of the lower canines. It appears very probable that these species are closely related if not identical, but it does not seem advisable to abandon the name *A. platycephalum* until the type can be more closely compared and the geographical position of the California specimen determined.

Aceratherium simplicidens (Cope).

Specific Characters.—Last superior molar with distinct remnant of the postsinus between the ectoloph and metaloph.

Type.—Portions of the second and third superior molars in the Museum of the University of Pennsylvania.

The type of this species is a fragment of the left maxillary bone containing the posterior portion of the second molar and the entire crown of the third molar. This was described by Professor Cope in 1891 as follows:¹

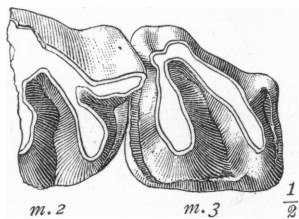


Figure 43. Type of *Aceratherium simplicidens* (Cope), showing portion of second and third upper molars of the left side. Collection of the University of Pennsylvania.

"*Cænopus simplicidens*, sp. nov.—Represented by the last two superior molars of the left side, with a probable humerus and femur. The molar teeth are one-third larger in linear dimensions than those of the *C. occidentalis* Leidy, and lack the external basal cingulum which is present in the corresponding teeth of that species. Internal cingulum wanting, but the anterior and posterior cingula present. The posterior limb of the metacone is represented in the posterior molar by a tubercle at the base of the crown, which rises into a low ridge, which soon disappears. It bounds a fossa with the posterior cingulum just behind it. Transverse crests simple, with a convexity representing the antecrochet.

Paracone distinct, separated by an open groove from the anterior angular cone. Both limbs of the metacone of the penultimate molar are well developed.

"*Measurements*.—Transverse diameter of M ii at anterior cross-crest, 48 mm.; ditto at posterior cross-crest, 38 mm.; ditto of M iii at anterior cross-crest, 45 mm.; antero-posterior diameter of ditto at inner base of crown, 42 mm."

This incomplete type was thus characterized by features which we now find to be invalid as specific characters. The most distinctive one is the vestige of the postsinus, which is also observed in the last upper molar of *A. platycephalum*, and occasionally as a reversion in *A. tridactylum* (No. 8088). The species is thus of very doubtful validity.

¹ American Naturalist, January, 1891, p. 48.

3.—SECOND SERIES.

Aceratherium copei, sp. nov.

PLATE XV.

Specific Characters.—Dentition, I^2 , C^{1-0} , Pm^4 , M^3 . Second superior incisor large, third superior incisor smaller. *Superior canines* present in immature skulls, shed in adult. Second superior premolar with two complete crests. Third and fourth upper premolars with strong tetartocone spurs united chiefly with protoloph. Internal cingulum faint.

Type.—Skull No. 522, Am. Mus. Coll. *Cotype*, skull No. 521, Am. Mus. Coll. These skulls were originally described by the writer (1894, p. 203) as belonging to *A. mite*. They are now named in honor of the late Professor Edward D. Cope.

Geological Level.—The types of this species, and other remains belonging to the same, all come from the base of the Oreodon Beds, on the stratum just above that in which the type of *A. trigonodum* was found.

This species is now seen to be clearly distinguished from the two preceding, *A. mite* and *A. trigonodum*, by the special character of its third and fourth upper premolars in which the tetartocone unites distinctly with the protoloph, rather than with the metaloph, as well as by the early loss of its superior canines. It is apparently a direct ancestor of *A. occidentale* and *A. tridactylum*.

DENTAL CHARACTERS.

We proceed to the examination of the dentition as exhibited in the two remarkably perfect skulls obtained by the American Museum Expedition of 1891.

Immature Dentition.—The immature condition of the teeth in this species is beautifully shown in the American Museum specimen No. 521, as represented in Fig. 44 *B*, and in Plate XIII, Fig. 4. The cutting teeth, incisors and canines agree in size with the alveoli observed in the adult skull (No. 522), and certainly represent the *permanent* or second series. The measurements are: Median incisors, 22×10 ; lateral incisors, 15×7 ; canine, 10×6 mm. The incisors have the characteristic elongate and flattened section, and the canine is much smaller than in *L. trigonodum* and somewhat incisiform, being flattened upon the internal surface and convex upon the outer surface.

It appears that the three anterior premolars ($pm1-3$) belong probably to the precociously-developed permanent or second series, because, first, the

excavation of the maxillary bone above these teeth shows no traces of successional teeth, and, second, they agree closely in form and size with the two corresponding teeth in the adult skull. In fact, as far as the first three premolars are concerned, the only difference between their form in the immature and mature skulls (Fig. 44, *A*) is that p^3 in the immature skull

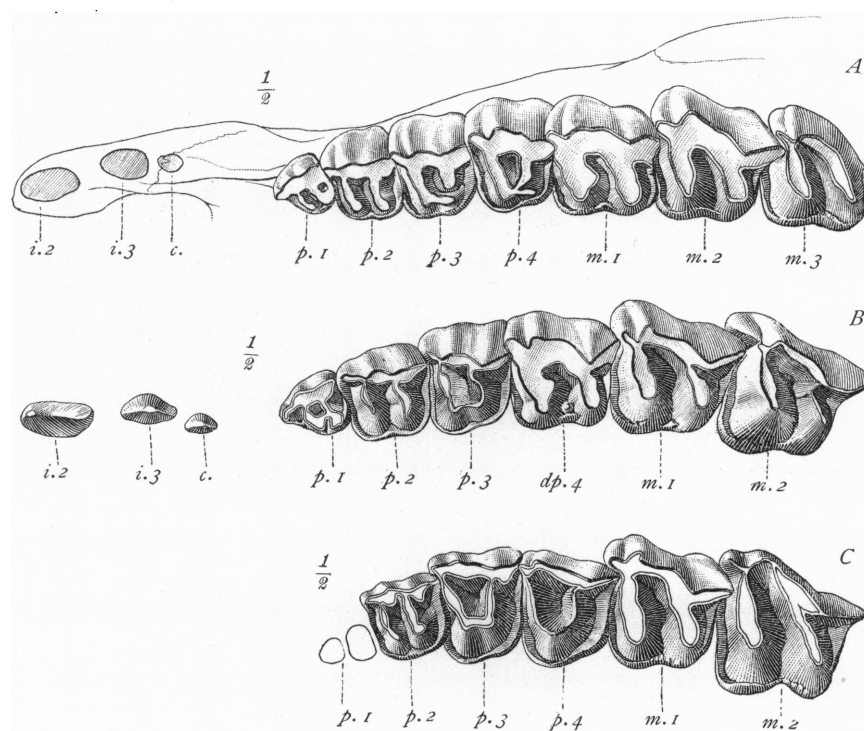


Figure 44. Milk and permanent premolars. Upper dentition of the left side of : *C*, *Lep-taceratherium trigonodum*, type specimen (No. 528) ; *B*, *Aceratherium copei*, showing fourth milk premolar dp^4 (No. 521) ; *A*, *Aceratherium copei*, showing mature dentition (No. 522). Collection of the American Museum of Natural History.

does not exhibit the hooked protoloph seen in p^3 in the mature skull, as better seen by a comparison of Figs. 3 and 4, Plate XIII. It resembles, however, the corresponding tooth in Cope's mature cotype of *A. mite* (see Fig. 2), and thus the form of the crests in p^3 may be a somewhat variable character.

The fourth premolar, on the other hand, is undoubtedly a milk or first series tooth, because it has a successional tooth in the maxilla above it, besides being completely molariform in structure with a well-marked antecrochet. In some modern Rhinoceroses, as observed by Lydekker,¹ the first premolar is variable in the adult and is sometimes a persistent milk tooth.

In this immature specimen of *A. copei*, therefore, p^1 , p^2 and p^3 do not appear to be persistent milk teeth, but to represent precociously-developed

¹ Catalogue of Fossil Mammalia in British Museum, Part III, 1886, p. 91.

permanent teeth, for the two reasons given above. This interpretation would be consistent with the unique fact that the anterior premolars become molari-form more rapidly than the posterior.

This evidence is to be contrasted with that seen in an immature skull of *A. occidentale* (No. 1125) as shown in a comparison of Figs. 5 and 6, Plate XIII, which certainly exhibits three milk teeth (d_2 , d_3 , d_4) followed by a complete succession of four permanent teeth, as described below.

COMPARATIVE MEASUREMENTS OF TEETH.

	No. 522.	No. 521 juv.
	MM.	MM.
Premolars.....	78	..
Molars.....	84	..
Molar-premolar series.....	162	92

Mature Dentition.—In the mature maxilla the shed canine is represented only by a vestigial alveolus. The adult grinding teeth are beautifully shown in the American Museum specimen, No. 522, as represented in Plate XIII, Fig. 3, and in Plate XV, Fig. 17. As already noted, the first and second premolars are similar to those in the young skull. The third and fourth premolars are very similar to each other; each has a strong protoloph, which sends backwards a spur which swells into a postero-internal cusp or ‘tetartocone.’ This tetartocone is somewhat larger and more robust in p^3 than in p^4 . The metaloph does not unite with the protoloph or tetartocone until well worn down, but forms a true half-crest, joining upon extreme wear not with the tetartocone but with the protoloph. This shows conclusively that the tetartocone is in no way a product of the metaloph in this species, but is budded off from the protoloph. It is clearly distinguished from *A. mite* and *L. trigonodum*.

The true molars have a variably defined internal cingulum upon the protoloph, which extends around into a strong anterior cingulum. The ‘ante-crochet’ is well indicated at the *base* of the protoloph, so that it is most apparent in the first molar in which the protoloph is worn to the base, but it is really almost as strong in the second molar and only a degree less so in the third molar.

COMPARATIVE MEASUREMENTS OF SKULLS.

	No. 522.	No. 521.
	MM.	MM.
Length : nasals to occipital crest.....	405	..
premaxillary tips to condyles.....	405	400
Width : zygomatic arches.....	195	165
Height : occiput from below condyles.....	114	..
Breadth : occiput across paroccipital process.....	118	..

CRANIAL CHARACTERS.

The two skulls in the American Museum collection are very completely preserved, but it is somewhat difficult either to figure or describe them with perfect accuracy, because they are vertically crushed. Experience shows that the entire proportions of a skull are so profoundly altered by vertical or lateral crushing that one is apt to be widely misled. Thus in the study of the otherwise excellent figures of skull No. 522, in Plate XV, considerable allowance must be made for flattening in the side view and broadening in the top view. In other words, the *A. copei* skull was higher and narrower than here represented. It is doubtful also whether the premaxillaries are quite in contact with the nasals, as represented in Plate XV, Fig. 15; the sutural lines apparently indicate contact. In the young skull (No. 521) there is apparently no such contact.

In general the skull is delicately proportioned with a rather light sagittal crest, arched naso-frontal contour, sharply pointed and laterally notched nasals, a rather low broad occiput, orbits placed well forwards, and a slender zygomatic arch.

Seen from the side (Plate XV, Fig. 15) the nasals do not reach as far forwards as the premaxillaries; they are deeply notched laterally. The premaxillaries are stout, and apparently come into a narrow contact with the nasals superiorly. The infra-orbital foramen is placed immediately above the second premolar. The lachrymal borders are indeterminate; they apparently extend well upon the face; the lachrymal is notched at the lower anterior rim of the orbit. The centre of the orbit is exactly midway between the premaxillary tips and the occipital condyles. The external auditory meatus is open inferiorly. The paroccipital processes (best preserved in Skull No. 521) are long and slender. There is apparently no exposure of the mastoid portion of the petrotic. Possibly as a result of crushing, the occipital condyles are only slightly above the level of the molar teeth.

Viewed from above (Plate XV, Fig. 14) the proportions of the facial and cranial bones are indicated in the linear measurements taken in the median line: nasals, 150; frontals, 115; parietals, 103; occipitals, 27 mm. The nasals resemble those of *Hyrachyus agrarius* in the deep lateral notch; the upper surfaces are perfectly smooth. The frontals are short, and indent the nasals sharply in the median line. The occipitals form the entire upper and posterior portion of the cranium; the occipital crest is indented superiorly. The parietals are characterized by numerous nutrient foramina. The sagittal crest is quite distinctive; it is marked by a shallow median groove, and in the mid-region of the parietals diverges into the well-defined supra-orbital ridges, which extend almost to the overhanging supraorbital processes of the frontals.

The height of the occiput is about equal to the breadth when measured across the paroccipital processes. Superiorly the occiput is slender, deeply concave and slightly overhanging the condyles.

In inferior view (Plate XV, Fig. 17) the premaxillaries are seen to be quite separate in the median line; the alveolus of the median incisor is 18 mm., and that of the lateral incisor, 12 mm. The alveolus of the aborted canine is represented by a shallow depression upon the maxillo-premaxillary suture; behind this is a diastema, 31 mm. There are apparently no posterior palatine foramina. The posterior nares opens between the second and third molars. The pterygoids are short and rather shallow. The foramen ovale is separated by a rather narrow (7 mm.) bony bridge from the foramen lacerum medium. The periotics are not well preserved, but there is exhibited in both skulls (Nos. 522, 521) a very characteristic tubular projection from the posterior wall of the foramen lacerum posterius, represented upon the lower side of Fig. 17.

***Aceratherium occidentale* (Leidy).**

PLATE XVI; PLATE XIII, FIGS. 5, 6, 7; PLATE XIX, FIG. 9.

Specific Characters.—Dentition, I_1^2 , C_1^0 , Pm_{4-3}^4 , M_3^3 . (a) Lateral upper incisors of medium size. (b) Upper canines wanting in deciduous and permanent series; lower canines with crowns of medium length, subtriangular, semiprocumbent. (c) Upper premolars: third premolar with complete metaloph early confluent with protoloph; fourth premolar with tetartocone of metaloph springing from protoloph, except in individuals of 'Upper Beds,' in which metaloph appears as a distinct crest when unworn. (d) Upper molars: 'antecrochet' developing upon first and second molars, feeble upon third molar; third molar with ectoloph and metaloph completely confluent. (e) Skull rather high and narrow; nasals long and smooth; upper contour, in profile a waving line; sagittal crest confined to posterior region of cranium; postglenoid and posttympanic processes approximated but not in contact; occiput narrow, rather elevated.

Type.—Original type indeterminate. Cotype Skull, No. 114, National Museum, Washington.

This classic species of Leidy was the first Rhinoceros discovered in this country. It is highly characteristic of the Middle Oligocene or 'Oreodon' level, and it extends throughout the entire 170 feet of vertical deposition of these Beds. This deposition represents a very long period of time, and as we pass from the lower to the upper levels, the *A. occidentale* exhibits a steady evolution through stages which might well be considered of specific value, as seen in a comparison of the molar series in Figs. 5 and 7, Plate XIII; also of the premolars in Fig. 47. It is not desirable to separate these stages into species.

A large number of skulls, including two belonging to very young individuals, collected by the American Museum Expeditions of 1891 and 1892, afford materials for a complete definition and characterization of this species.

A. occidentale is readily distinguished from *L. trigonodum* and from *A. mite* by the absence of canines in both the milk and adult series. The form of the skull approximates that of *A. tridactylum*, to which this species is undoubtedly ancestral, but the relatively large size of the lateral upper incisors is in great contrast with the reduced condition of these teeth in *A. tridactylum*, as shown in Plate XVII.

HISTORICAL NOTES.

1. In the 'Proceedings' of the Philadelphia Academy of 1850, p. 119, we find Leidy's first mention of this species, in reference to a number of isolated upper molars, as follows: "Dr. Leidy exhibited several molar teeth and fragments of maxillæ of a fossil Rhinoceros, from Missouri territory, received from the Smithsonian Institution through Prof. Baird, which indicate a species little more than half the size of the recent *R. indicus*. He characterized it under the name of *R. occidentalis*."

2. The second mention was in 1851, and is found upon page 276 of the same volume of the 'Proceedings,' giving measurements but no description of the inferior molars.

3. The third mention, upon p. 331 of the same volume (1851), relating to remains found in Nebraska, is as follows: "Dr. Leidy made some remarks upon the two species of Rhinoceros from Nebraska, which he has named *R. nebrascensis* and *R. occidentalis*, and said he had satisfied himself that they both belonged to the subgenus *Acerotherium* *Kaup*, a good character of distinction of which, in the teeth, is the *presence of a well-developed basal ridge*." (Italics are our own.)

4. In the following year (1852) Leidy published his 'Description of the Remains of Extinct Mammalia and Chelonia from Nebraska Territory, collected during the Geological Survey under the direction of Dr. D. D. Owen,'¹ in which (p. 552) he says: "The species was first established upon several fragments of teeth, and afterward confirmed by obtaining several entire teeth." He proceeds to describe a skull, fragments of lower jaws and the distal part of a femur in the collection of Dr. Owen. In describing the upper molars he says (p. 554): "They all possess a basal cingulum, which is, however, but feebly developed on the outer side of the anterior

¹ 'Geological Survey of Iowa, Wisconsin and Minnesota,' Philadelphia, 1852.

half of the fifth and sixth molars, and is obsolete on part of the internal lobes of the same teeth." This passage directly contradicts Leidy's own sub-generic description which we have italicised in the passage quoted above. The skull is a fine type, and is fully described and figured.

It is evident from our present fuller knowledge, first, that these four notices were possibly, if not probably, based upon specimens belonging to four different species; second, that the three earlier specimens are, according to the rules of nomenclature, undefined and indeterminable; third, that the fourth notice, namely, of the skull in the Owen's Collection, established this skull as a cotype, and the species and the specific name should date from this description. Fortunately, this cotype is preserved in the National Museum at Washington (No. 114).¹ Subsequent writers have not observed closely the characters of this type, so that there is much confusion as regards the specimens referred to *A. occidentale*, and the species requires accurate definition.²

CHARACTERS OF THE COTYPE SKULL.

The type *skull* is a fully adult individual (Coll. National Museum, No. 114). It originally lacked the ends of the nasals, the occiput and the tips of the premaxillaries; the zygomatic arches have been lost in subsequent handling. The worn condition of the third and fourth superior premolars prevents a precise description; the most distinctive feature of the fourth pre-

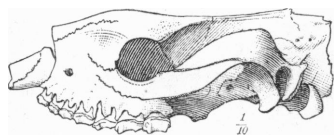


Figure 45. *Aceratherium occidentale*, cotype, skull (No. 114) in the Collection of the National Museum, Washington. Since originally figured, this skull has been injured and certain portions lost.

molar is that the metaloph turns forward to the protoloph, and the postero-internal lobe, or tetartocone, is a backward spur. In lateral or profile view the straight superior border of the skull is the most striking feature, but there is a slight posterior rise, indicating that the occiput was slightly elevated. The nasals, so far as preserved, are straight and smooth. The superior aspect is marked by great breadth between the orbits, fairly well-marked supratemporal ridges converging very gradually into a short, thick sagittal crest, which is confined to the posterior part of the cranium.

The basal view shows narrow posterior nares and short pterygoids. The ovale is very close to the lacerum medium. The *dentition* is remarkable for the primitive condition of the premolars, especially the fourth, which shows convergent and early confluent crests and a bifid internal lobe, for, as far as can be seen (compare Fig. 47 B), the postero-internal lobe is still mainly a

¹ By direction of the late Director, G. Brown Goode, it was kindly loaned to the writer.

² Leidy's most perfect figures and descriptions of this type are in his Memoir: 'Extinct Mammalia of Dakota and Nebraska,' 1869, p. 220, Pl. xxii.

backward spur from the protoloph instead of a part of the metaloph. The first and second premolars have well-developed internal crests. The cingulum, which is strong upon the premolars, is obsolete upon the inner faces of the protoloph and metaloph in the molars; the outer faces of the molars are faintly cingulate.

SKULLS IN THE AMERICAN MUSEUM COLLECTIONS OF 1891 AND 1892.

The American Museum Specimen No. 1107, consisting of the upper premolar-molar series from the '*Lower Oreodon Beds*,' agrees precisely in size and in every other detail with Leidy's type. It is important because it probably enables us to locate the exact level in which the type was found, and also (as represented in Plate XIII, Fig. 5) gives us the exact state of evolution of the fourth premolar which cannot be ascertained upon the type.

The species is moreover represented in the Museum collection by six skulls and numerous lower jaws. The skulls were found in four levels, namely, the '*Metamynodon*,' '*Lower*,' '*Middle*' and '*Upper Oreodon*' levels, as shown in the stratigraphical table upon page 129, also in the subjoined table. The total thickness of these four levels is about 170 feet.

Geological Levels	Metamynodon Beds.	Lower Oreodon Beds.	Middle Oreodon Beds.		Upper Oreodon Beds.		
Catalogue Nos. American Museum Collection	No. 1144.	Leidy's No. Type. 1107.	No. 1108.	No. 532.	No. 537.	No. 1123.	No. 535.
Superior molar-premolar series	115	182 ..	185	197	191	194	..
" molar series.	115	102 103	101	..	105	106	112
Condyles to tips of premaxillaries.	465	? 460	? 460	485	475	..
Height of occiput	135	?	140	? ..	160
Breadth of zygomatic arches	? 196	230	220	..	238	212

The increase in the length of the skull from 460 mm. to 485 mm., although not very great, probably marks the steady increase in size leading up to the larger species of the '*Protoceras Beds*,' namely, *A. tridactylum*.

General Characters.—These are well shown in the composition drawing of Plate XVI, and in comparison with other skulls in Fig. 33. These compositions are from the male skulls of the '*Middle Oreodon*' level, and are somewhat more highly evolved than the *A. occidentale* type specimen of Leidy.

In lateral view (No. 537) the nasals extend as far forward as the premaxillaries; they are pointed towards the tip, and exhibit a distinct lateral

notch as in *A. mite*, and in *Hyrachyus agrarius*; they rise in a gentle curve and then sink above the orbits. The marked sexual characters of the nasals and of the skull in general are enumerated below. The premaxillaries do not reach the nasals. The maxillaries exhibit two slight lateral depressions, and are deeply indented by the large lachrymals. The lachrymal notch is at the lower anterior border, and above it is a small rugose knob, also characteristic of *A. tridactylum*. The malars extend to the antero-inferior angle of the orbit. The orbits are slightly in advance of the middle of the skull; behind them the supratemporal ridges rise with the occiput, which is considerably above the level of the nasals and slightly overhangs the condyles. There are from one to three parietal foramina. The zygomatic arches rise rapidly posteriorly; they diverge very slightly opposite the glenoid fossæ. The posttympanics are close to the postglenoids, but never quite in contact. The paroccipital processes are very long and slender; extending below the level of the postglenoids.

In superior view the upper surface of the facial region is diamond-shaped; the nasals appear perfectly smooth and pointed at the extremities. The frontals widen greatly, and are somewhat rugose above the orbits; the temporal ridges converge very gradually to the posterior part of the cranium, where they suddenly diverge into a narrow sagittal plate, which is highly characteristic of this species and of *A. tridactylum*, and join the rather narrow supraoccipital border.

The occipital view is very distinctive. The condyles are of great vertical depth. The occiput is of moderate height, narrow in the mid-section and spreading above.

In basal view the premaxillaries are seen to be barely in contact in the median line, and to enclose the very open anterior palatine foramina. The palate opens opposite the second molar, and the pterygoids are short. The f. ovale is slightly in front and to the outside of the f. lacerum medium, and the periotic bones are deeply depressed and do not separate this foramen sharply from the f. lacerum posterius. The postglenoid processes are placed on the inner posterior angles of the glenoid fossæ, with their greatest diameter fore and aft. The basi-occipitals are keeled in the median line and rugose at their junction with the basisphenoids.

IMMATURE SKULL AND DENTITION.

With the collection is a perfectly-preserved baby *Aceratherium* skull (No. 534) ten inches long (35 cm.), with the teeth, lower jaws and hyoid bones complete; this is from the 'Upper Oreodon Beds.' A second baby skull (No. 1125), less perfect, is from the 'Metamynodon' or 'Lower Oreodon

Bed' level. Both can be probably referred to *A. occidentale*, and are very important because they show the complete milk dentition. All the sutures in No. 534 are distinct. The nasals, frontals and parietals are of equal length. The upper posterior portion of the cranium is formed by the occipitals. The nasals extend laterally well down upon the sides of the face, but do not touch the premaxillaries. The junction of the posttympanic and paroccipital processes is very sharply defined, and there is no trace of the mastoid portion of the periotic upon the outer surface of the skull. The cerato-hyals are very long (11 cm.) and slender, and a portion of the left basi-hyal is preserved.

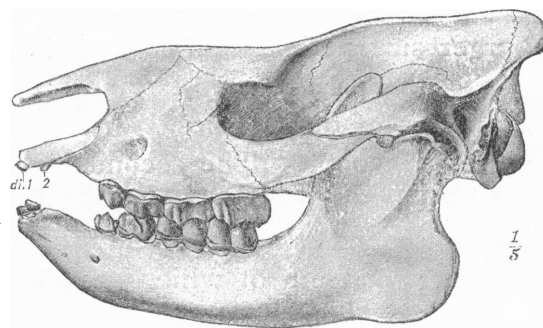


Figure 46. Lateral view of skull of Calf Rhinoceros, *A. occidentale*, No. 534. Collection American Museum of Natural History.

MILK DENTITION OF *A. OCCIDENTALE*.

PLATE XIII, FIGURE 6.

Skull No. 534 measures 340 mm. in total length, and it therefore represents a calf Rhinoceros, relatively much younger than the youngest specimen of *A. copei*. The young *A. copei* skull No. 521, described upon page 147, while retaining the fourth milk premolar and the superior permanent canine was, judging by its size, only a few months younger than the more mature skull, No. 522, with which it was compared.

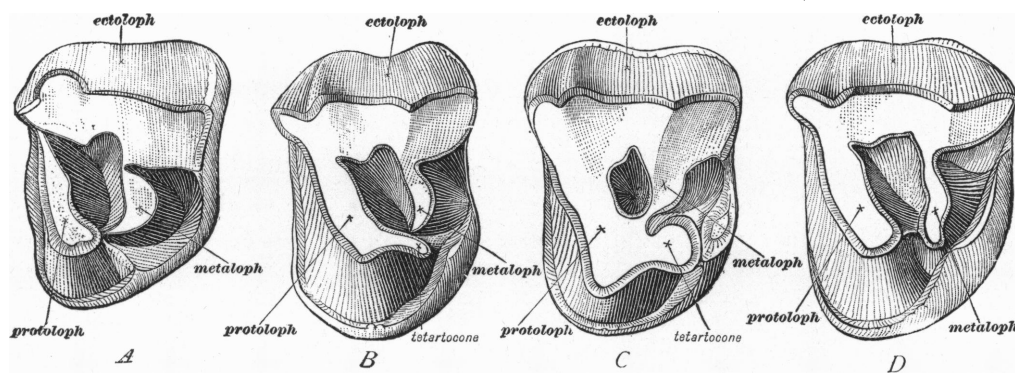
In this calf skull of *A. occidentale* (No. 534) we are therefore dealing with an animal, probably a month or so after birth, and accordingly find that the milk teeth are all in place; we have here apparently a full set of milk teeth, all of which will be replaced in the adult animal. The animal differs at once from the young *A. copei* in the entire absence of upper canines. The median incisors above are very small, with elongate or laterally compressed crowns. The lateral incisors are still smaller. In the lower jaw the median milk incisors present, in miniature, the same form as the permanent teeth, but the canines have very short and obtusely-pointed crowns. The first milk premolar has an elongate ectoloph and protoloph connected with the tetartocone, the metaloph being represented by a low spur. The second milk premolar has a vertical rib in the middle of the outer wall, internal to which is a distinct crista. The protoloph and metaloph are fully-developed

crests, and at the entrance of the medisinus is a prominent tubercle. The third milk premolar is completely molariform, the ectoloph exhibiting three costæ corresponding with the parastyle, paracone and metacone; the transverse crests are distinct and well developed. The fourth milk premolar is of larger size and substantially of the same form. The presence of the costa opposite the paracone is a primitive character which is not observed in the true molars of this species. In the lower jaw the first molar is a laterally-compressed tooth. The second is elongate but lacks the distinct transverse crests. The third is submolariform, and the fourth is fully molariform.

The second skull (No. 1125) is also of a calf of practically the same size, the milk teeth of which are shown in Plate XIII, Fig. 6. They exhibit substantially the same characters as the above, except that the first premolar has somewhat more irregular internal cusps and crests, and the second apparently lacks a crista.

ADULT DENTITION.

Even in the youngest skulls there is no trace of the superior canines. As shown in Fig. 34, the superior incisors are distinguished from those of *A. mite* by the enlargement of i^2 and the greater reduction of i^3 . The inferior incisors, i_3 , are spatulate with a sharp cutting edge reaching its highest point at the median line. The inferior canines in the males are robust, subtriangular teeth; the antero-external face is flattened; the postero-external face is rounded; the internal face is sharpened by wear against the enlarged upper incisors.



TYPICAL PREMOLAR METAMORPHOSIS.

Figure 47. Fourth superior premolars in four specimens of *Aceratherium occidentale*, taken from successive geological levels. Collection of the American Museum of Natural History. After Osborn and Wortman (1895).

The superior premolars require an elastic interpretation, since they present many phases of transformation towards the molar pattern. The first premolar exhibits a long ectoloph and two irregular transverse crests. The

second premolar invariably presents two complete transverse crests, which unite only after prolonged wear. The third premolar always presents two complete crests which unite somewhat earlier than those of p^2 . The fourth premolar, as we pass from the 'Lower' to the 'Upper Oreodon Beds,' exhibits stages in the transformation of the crests into molar form—the earlier stages resembling the ancestral *A. copei* type, the later stages exhibiting the succeeding *A. tridactylum* type, as clearly shown in the accompanying figures, and in Plate XIII.

The molar teeth are more constant in character. They vary in the development of the 'antecrochet,' which is as a rule very decided upon m^1 and much less conspicuous upon m^2 and m^3 . The third superior molar sometimes exhibits a shallow but distinct 'postsinus.'

The inferior premolars do not parallel the development of the superior, because the fourth pm^4 is upon the whole a much more distinctly molari-form tooth than the second (pm^2). The first premolar is vestigial, and has dropped out of all the jaws in the collection (although it is present in two jaws of *A. tridactylum*). The second premolar is a laterally compressed tooth with an inner and outer spur from the central portion of the crown. The third premolar exhibits two complete crescents, and the outer median spur opposite the anterior crescent. The fourth has the breadth, proportions and crests of a true molar.

SEXUAL CHARACTERS.

In comparing various skulls of *A. occidentale* we find considerable variations in the size of the lower canine teeth. In certain skulls, which are presumably females, these teeth are short and obtuse. In others, probably males, they are elongate and triangular. Unfortunately we have very few specimens in which the jaws are associated with the skulls in such a manner as to enable us to correlate these dental characters with those of the skull, as we shall do in the case of *A. tridactylum*. We observe considerable differences, however, in the form of the nasals. In No. 704, a young and fragmentary specimen from the 'Oreodon Beds,' which probably belongs to this species, the nasals are straight and slender, with a marked lateral notch and separate in the median line. The section is thin and the contour strongly resembles that of the nasals of *A. copei*. The same character is observed in the nasals of the fine skull, No. 1136, the nasals being perfectly smooth and somewhat more united in the median line, owing to the greater age of this individual. In No. 1144, an adult from the 'Metamynodon Beds,' the nasals are of medium thickness. In No. 1123, from the 'Upper Oreodon Beds,' the nasals are considerably thickened and arch from side to side

upon the upper surface, so that there is a slight longitudinal median groove between the nasals, as seen from above. In No. 532, also catalogued 'Oreodon Beds,' the nasals are extremely long, thin in section and gradually tapering to the extremities, being partly separate in the median line, although this is a very old individual. It thus appears in general that there are two types of nasals, those of thin and those of thicker section and transversely arched above. The latter type probably characterizes the males, and is progressively developed as they ascend to the Upper or 'Protoceras Beds.' In the females the nasals apparently remain long and slender and not united in the median line.

*Aceratherium tridactylum*¹ Osborn.

PLATE XVII; PLATE XIII, Fig. 8; PLATE XIX, Fig. 30; PLATE XX.

SYN.—*Diceratherium proavatum* HATCHER.

Dentition.— I_2^2 , C_1^0 , Pm_4^{1-3} , M_3^3 . (a) Upper lateral *incisors* small. (b) Lower canines long, subtriangular, semi-procumbent. (c) *Upper premolars*, first, second and third with entirely distinct and complete protoloph and metaloph, fourth with complete metaloph which early coalesces with protoloph. Anterior enamel wall of metaloph and internal wall of ectoloph more or less crenulate in both molars and premolars. (d) *Upper Molars*: External and internal cingula variable. 'Antecrochet' strong upon m^{1-2} . Metaconule bold, well marked at base of metaloph in m^{1-2} . 'Crista' incipient in m^{1-2} . (e) *Skull*: Nasals arched, thin and smooth in females, thick and rugose in males; occiput very elevated; postglenoid-posttympanic contact broad in old males; sagittal crest broad and very short antero-posteriorly; zygomata arching widely posteriorly.

Type.—A complete skeleton, No. 538, American Museum.

Materials.—This species was discovered and described in 1893 from a remarkably perfect individual, the skeleton of which is figured in Plate XX. The animal was found outstretched in the coarse green sandstones of the 'Protoceras Beds,' or topmost division of the White River Oligocene, and described as follows:²

.....
"*Aceratherium tridactylum*, sp. nov. *General Characters*.— I_2^2 , C_1^0 , P_4^4 , M_3^3 . Digits 3-3. Vertebrae, D 19, L 5, S 3, C 21. Occiput elevated. Postglenoid and posttympanic enclose auditory meatus inferiorly. Superior molars with strong 'antecrochet' and 'crochet' feeble or absent. First upper premolar well developed. Incomplete cingulum upon inner face of true molars. Occiput high and narrow.

"The type of this new species is a complete skeleton in excellent preservation, which was discovered by Mr. Peterson of the Museum party, and has now been mounted for exhibition by

¹ Bull. Am. Mus. Nat. Hist., Vol. V, April 29, 1893, pp. 85-6

² American Museum Bulletin, Vol. V, April 29, 1893, p. 85.—Features of the description which are unessential or incorrect have been omitted in this quotation.

Mr. Hermann. The only parts lacking are the left forelimb, a few of the ribs, and the sternal bones. All the other parts are complete, the vertebral column being perfect to the tip of the tail.

"The skeleton measures seven feet nine inches in length, and four feet in height to the top of the lumbar vertebral spines. There are nineteen dorsal, five lumbar and three sacral vertebrae. The pelvis is long and rather slender, and the limbs are of an intermediate type, heavier than in *A. occidentale* and much longer than in the Upper Miocene *A. fossiger*. There are only three digits in the manus, hence the name *tridactylum*, there being no trace of the fifth digit, which is so characteristic of the Lower Miocene Rhinoceroses of America and Europe, with the possible exception of *A. mite* Cope.

"The total length of the skull is 51 centimeters, while in *A. occidentale* it measures 44. The occiput is high and rather narrow...the upper line of the skull thus curves upwards, and the sagittal crest is considerably shortened. Another progressive feature is that the molars show, besides the strong 'antecrochet,' a beginning of the 'crochet,' which is wholly undeveloped in *A. occidentale*. The median upper incisors are much larger than the outer pair, and the lower canines are correspondingly enlarged. The first lower premolar (pm_1) is rudimentary or wanting.

"Another distinctive feature of the skull is the union of the postglenoid and posttympanic processes to enclose the external auditory meatus inferiorly.".....

Owing to the paired convexities and rugosities upon the nasals in the skull of this and other types, the animal was reported by letter from the field as a *Diceratherium*, and this conjecture as to its probable relationship has subsequently proved to be correct from evidence brought forward by Hatcher (1897) and the writer in the present memoir. Another skull belonging to an animal of the same type (No. 541) was described at the same time. Altogether, the American Museum expeditions secured ten skulls.

Comparison with A. occidentale.—The species is at once seen to be a progressive form of *Aceratherium occidentale* in the same line of descent. It agrees with this ancestor in many details, such as the subtriangular form and oblique position of the lower canines, the very frequent presence of both internal and external cingula upon the molars, and in minor superficial characters of the skull, as seen in a comparison of Plates XVI and XVII. It differs from *A. occidentale* in the marked reduction of the lateral upper incisor, in the greater arching of the nasals, in the more elevated occiput, in the usual closure of the external auditory meatus inferiorly, in the crenulation of the upper premolar and molar enamel, in the incipient development of the 'crochet' and 'crista' upon the molars, in the less distinctly triangular section of the canines, in the widening out of the supratemporal ridges and consequent flattening of the cranium, and in the development of rudimentary paired rugosities on the nasals of old males.

DENTITION.

Incisors and Canines.—Both the upper incisors are well preserved in the type and in Skull No. 1126. The median incisor is from two and one-half to three times the diameter of the lateral incisor (Fig. 34, text). The lateral

incisor is in some skulls (No. 1122) extremely reduced, while the median incisor is a strong and vigorous tooth, relatively larger than in *A. occidentale*, having evidently profited by the reduction of its neighbor.

Premolars and Molars.—The grinding teeth of the type specimen have not been completely removed from the matrix. The following description of the molars is from another series (Plate XIII, Fig. 8), belonging in skull No. 1120.

The first upper premolar is a stout tooth with an elongate ectoloph, short protoloph, and long recurved metaloph. The second and third premolars are similar in pattern, with two complete crests quite distinct internally. The fourth premolar is less fully quadrate in form, and is far from being completely molariform, for the metaloph, although a complete crest, is very slender and becomes early confluent by wear with the protoloph; this feature is seen in all individuals. The anterior enamel wall of the metaloph shows a faint crenulation, and this is also observed on the inner enamel wall of the ectoloph, or at the head of the medisinus.

This crenulation is also characteristic of the corresponding enamel surfaces in the molars and appears to be a readily distinguishable specific character; it varies in different skulls, and is sometimes a very conspicuous feature of the premolars, as in No. 1122 (see Plate XIII, Fig. 8). In the teeth we are especially describing (No. 1120) the internal and external cingula of the molars are rather feebly developed; in certain individuals, however (Nos. 1122, 1137, 1137A), they are well marked; the cingulum is therefore not a constant specific character, nor is it apparently a *sexual* character, for it appears equally strong in male and female skulls. The incipient 'crista' is well marked. The compression of the inner basal portion of the metaloph to form the 'inner crochet' or fold between the hypocone and metacone is well defined in m^1 and m^2 , and upon extreme wear this becomes a conspicuous feature; it is observed in every individual, and is a constant specific character. In the third molar of No. 1120 is seen a very slight median elevation of the cingulum at the entrance of the median valley; this cingule is somewhat more marked in skull No. 1111, and constitutes a prominent pointed cusp in skull No. 1124. It is an inconstant character, but it is noteworthy because it occurs in the *Diceratherium* of the John Day, constituting additional ground for the supposition that this animal is related to *Diceratherium*.

Among the distinctive characters of the lower grinding teeth is the variability and usual absence of the first lower premolar, as already observed in *A. occidentale*. In certain jaws (Nos. 543, 1109) this tooth is seen upon one side and not upon the other. The crests of the lower premolars do not exhibit a very marked advance upon the characters already observed in *A. occidentale*.

COMPARATIVE MEASUREMENTS OF SKULLS.

(Sex as far as distinguishable : ♂ Male, ♀ Female.)

American Museum Nos.	♂ 538 TYPE.	♂ 541	♂ 1126	1111	♂ 1137A	♀ 1137	♀ 1122	♀ 1121	♂ 1124	? ♂ 1120
Superior molar-premolar } series.....	212	207	205	212			205	183+	197	218
Superior true molars.....	121	112+	? 115	111	119	115	113	110+	101	122
Inferior molar-premolar } series.....										
Condyles to tips of pre- } maxillaries.....	510	475	485				475+	425+		
Height of occiput.....	175	182	180				140	150	133+	
Breadth of occiput.....	100+	104	? 80				76	104	90+	
Zygomatic arches, breadth,		265	? 246	246			237	255	282-	308

The sign + or - indicates that measurements (given in millimeters) have probably been increased or diminished by crushing of skull.

The skull of the type (No. 538) is finely shown in *lateral* view in Plate XVII. The superior view is imperfect because crushed, and the basal view has not been cleared from the matrix. In lateral view (No. 538) the nasals are long, well arched from side to side, and antero-posteriorly; they have a double longitudinal convexity which is increased by lateral crushing, and they exhibit slight lateral rugosities; in front they suddenly contract and extend forwards as paired tapering cylinders; they extend well down at the sides of the anterior nares quite close to the premaxillary suture. The infra-orbital portions of the frontals are rugose and overhanging. The lachrymals have a very extended exposure, and the knob, which we observed as a rudiment upon the front border of *A. occidentale*, is now very prominent. Back of the orbits the upper border of the cranium rises very sharply and the supra-temporal crests are rugose and clearly defined. The parietals upon either side of the high and narrow cranium present a waving surface and two nutrient foramina. The zygomatic arches also rise sharply and swell suddenly outwards above the glenoid fossæ, a feature which is highly characteristic of this species, and most sharply marked in the males. Other progressive features are the strongly internal position of the postglenoid process; the extended junction of the postglenoid and posttympanic processes below the auditory meatus; the long and slender paroccipital processes, and the marked shortening of the skull behind the auditory meatus—a feature which is somewhat exaggerated in the perspective drawing in Plate XVIII. In *superior* view the supratemporal ridges come together so far back that the sagittal crest is reduced to an extremely short area between these ridges and the supraoccipital plate. The occiput is extremely high and narrow, constricted in the mid-region and spreading superiorly.

The lower jaw exhibits a well-developed post-cotyloid process, a prominent angle and slender coronoid process.

SEXUAL CHARACTERS.

The above characters are mainly seen in the type skull, No. 538, which, judging from the large size of the lower canines, apparently belonged to a young male, an inference which is strengthened by the presence of

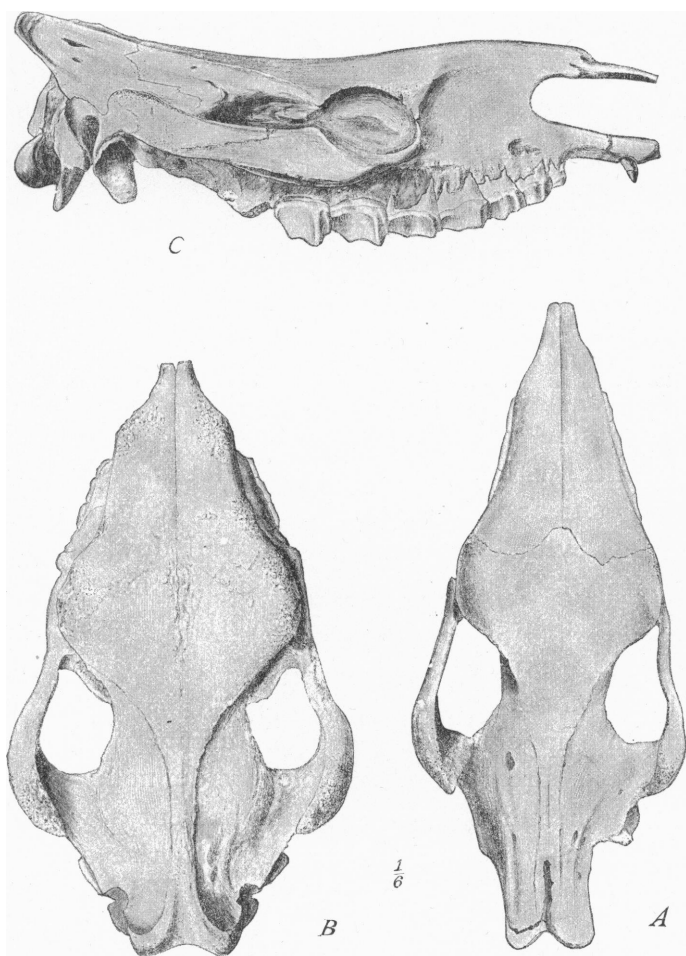


Figure 48. Illustrating the sexual characters in the skulls of *Acraethium tridactylum*:

A, C, Superior and lateral views of skull of adult female (No. 1122), showing the elongation of the nasals, absence of rugosities, marked reduction of lateral incisors. This skull is crushed laterally.

B, Skull of an old male (No. 1124), showing abbreviation of nasals, lateral rugosities of same character as in type of *D. proavatum*, rugosities above orbits and upon zygomatic arches. This skull is crushed vertically.

All from the Protoceras Beds. Collection of American Museum of Natural History.

very faint rugosities upon the nasals, and the slightly rugose character of the supraciliary ridges and outer portions of the zygomatic arches. The observations made upon *A. occidentale* (page 157), as to the sexual characters in these animals, are paralleled and confirmed in the more numerous and perfectly-preserved skulls of *A. tridactylum*.

Of the male skulls, the most extreme type is represented in No. 1124 (Fig. 48 B), an extremely aged male, with the molar teeth almost worn to the fangs. In this old animal not only the nasals but the whole upper surface of the cranium, the region above the eyes, the supratemporal ridges, the outer portion of the zygomatic arches, the angle of the jaw, are extremely rugose, or covered with exostoses. The nasals are considerably thickened and somewhat arched from side to side, terminating somewhat more obtusely than in the

female skulls. Skull No. 541, on the other hand, is a middle-aged male, and presents substantially the same characters as the type skull, No. 508. Nos. 1137, 1122, 1171, on the other hand, may be regarded as female skulls,

in which the nasals are long, pointed and slender, less arched from side to side, more delicate in section, more separate in the median line and without any rugosities. In these skulls the cranium is throughout less rugose, the supratemporal ridges, the zygomatic arches and the occiputs being of a less robust character, the postglenoid and posttympanic processes not uniting in some cases.

As the nasals, especially in the males, thicken with advancing age, this thickening and arching may be regarded as a progressive character, which will appear at earlier stages of development in the successors of *A. tridactylum*. Thus while Hatcher's conclusion, that this animal should be placed in the genus *Diceratherium*, is not sustained by the above demonstration that the variations in the nasals are sexual, the points he brings forward, especially as to the structure of the nasals, certainly tend to confirm the theory that *A. tridactylum* stands in the ancestral line of *Diceratherium*. We may regard his species, *Diceratherium proavium*, as based upon an adult male specimen of *A. tridactylum* with paired rugosities upon the nasals.¹

RESEMBLANCES TO *DICERATHERIUM*.

In addition to the prophetic thickening of the nasals, *A. tridactylum* shows many other characters which we find in *Diceratherium*, as seen in the fine skull (No. 7324) from the Cope Collection in the American Museum. This skull is probably from the upper portion of the John Day Beds, and thus represents a very advanced type with a very prominent pair of bony swellings upon the nasals. In the molar and premolar teeth of *Diceratherium* we notice the crenulation of the enamel at the head of the medisinus noted in *A. tridactylum* on page 160, also the tubercle at the entrance of the medisinus on the third superior molar. The zygomatic arches exhibit a sudden bulging posteriorly exactly as in *A. tridactylum*. The occiput is high and narrow, and the general form of the superior surface of the skull is similar, the proportions being dolichocephalic. In this species (*Diceratherium*

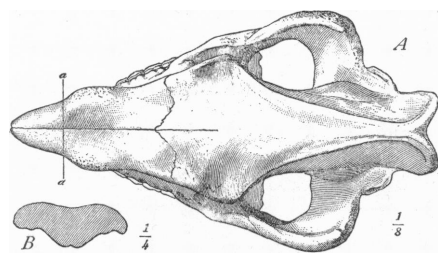


Figure 49. Superior view of type of *Diceratherium proavium* Hatcher (*Aceratherium tridactylum*), showing thickening and rugosity of nasals. After Hatcher (1897). Collection of E. M. Museum of Geology and Archæology, Princeton.

nanum Cope), however, the external auditory meatus is not closed below, this being one of the principal differences.

¹ In Mr. Hatcher's original description of this species in the 'American Geologist,' May, 1894, pages 360-1, there is a typographical error. This description should read, "no upper canines."

Description of Diceratherium proavium.—The first and second notices of this species by Hatcher were partly due to a misapprehension of the real characters of *A. tridactylum*, owing to certain inaccuracies in the figures and descriptions published by the present writer. They are also due to Hatcher's failure to realize the profound differences which are caused by age and by the vertical and lateral crushing of the skull; differences which are well illustrated in the male and female skulls of Fig. 48. None the less Hatcher has rendered a distinct service in his second paper (1897), in calling especial attention to the progressive strengthening of the nasals, as in the following paragraphs (1897, p. 313):

"Nasals very strong, partially coössified and bearing upon their upper and outer surfaces a pair of rugose prominences situated at about one-third the distance from their extremities to their junction with the frontals. These prominences resemble very much the rugosities supporting the nasal horns in many of the recent rhinoceroses, and doubtless served the same purpose in *D. proavium*. Behind this pair of rugosities the nasals are constricted, but posteriorly they expand again to meet the broad anterior border of the frontals. The fronto-nasal suture is but little in front of the orbit. In front of the pair of rugose elevations the nasals contract rapidly, and are directed downward and forward." Again he says (1897, p. 315): "Aside from the rugosities there are other evidences even more in favor of considering them as having borne horns; such as the great thickening of the nasals [shown in Figure 48 B] in order to give the necessary strength to support the horns, and the low, short and broad sagittal crest as shown in Fig. 1. Furthermore, the geological horizon (*Protoceras Beds*) in which the type was found is just that in which we expect to find the ancestor of the John Day form."

This species, *Aceratherium tridactylum*, therefore, belonging to what we have termed the Second Series, in all probability links the *A. copei* and *A. occidentale* in a most unexpected manner with the Diceratherinæ, giving us the American ancestry of the lateral pair-horned *Diceratherium* of the John Day or Lower Miocene.

In consequence we must look to members of the First Series for ancestors of the Miocene Aceratheres and true Rhinoceroses in the continuation of this research.

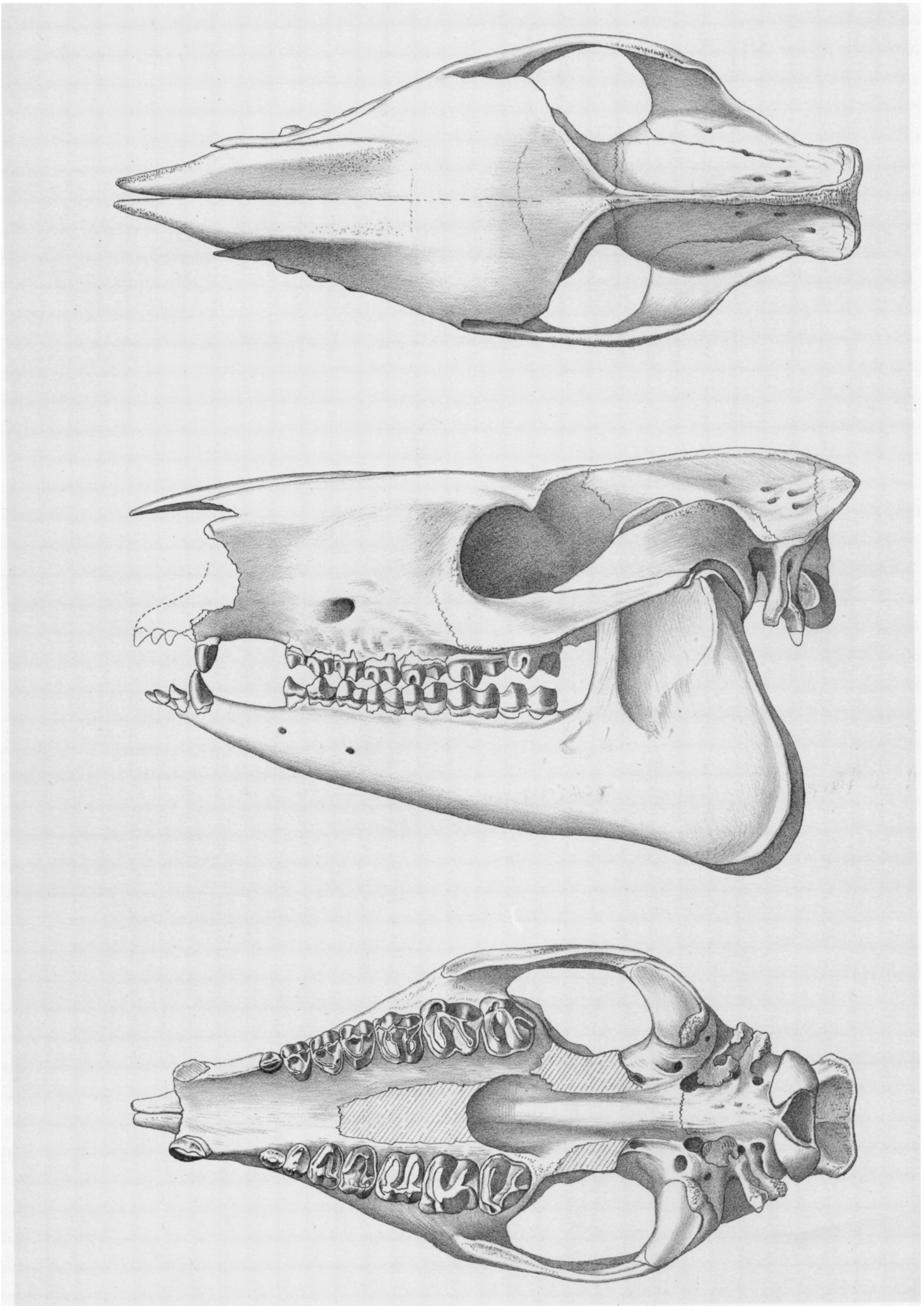
PLATE XIII.

EXPLANATION OF PLATE XIIA.

Hyrachyus agrarius.

One-half natural size.

Superior, lateral and inferior views of the skull of *Hyrachyus agrarius*, No. 1645, in the Collection of the American Museum of Natural History. A portion of the area between the orbit, nasals and canines has been restored, otherwise the skull is complete. This skull agrees in size with the occiput and angle of the jaw belonging to the skeleton of *H. (eximus) agrarius* from the Cope Collection, as represented in Fig. 1 (text). It has therefore been mounted with this skeleton in the American Museum, replacing the fragmentary skull. . . . Page 81.



HYRACHYUS AGRARIUS.

† Natural Size.

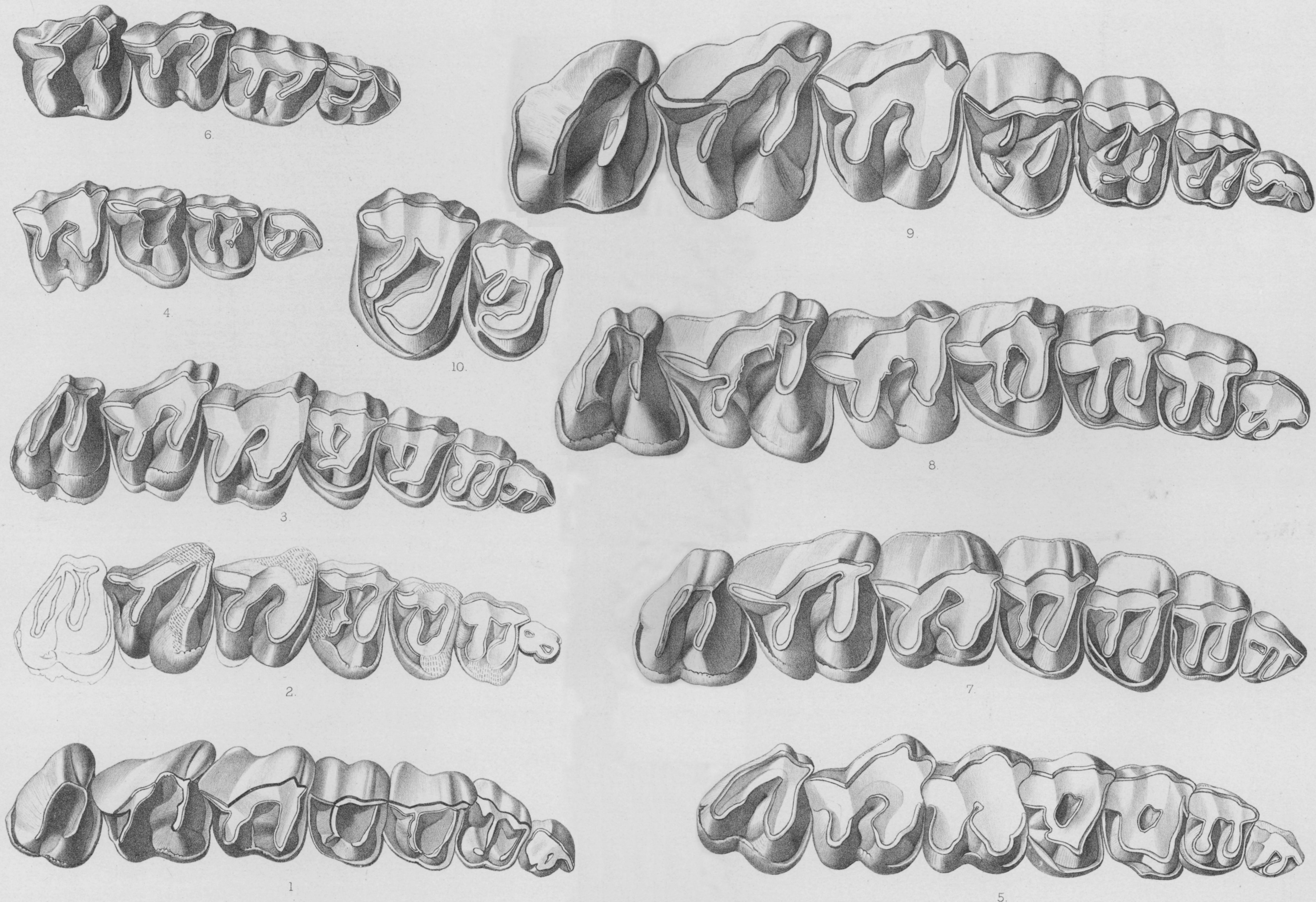
PLATE XIII.

EXPLANATION OF PLATE XIII.

Molar-Premolar Series of the Oligocene Aceratheres.

All natural size.

- Fig. 1.—**Leptaceratherium trigonodum.** Type specimen, showing the undeveloped condition of the premolar teeth. No. 528, in the Collection of the American Museum of Natural History.....Page 132.
- Fig. 2.—**Aceratherium mite.** Cotype, No. 6525, in the Cope Collection, American Museum of Natural History.....Page 136.
- Fig. 3.—**Aceratherium copei.** Exhibiting the differences between the third and fourth premolars and those of *A. mite*. No. 522, in the Collection of the American Museum of Natural History.....Page 146.
- Fig. 4.—**Aceratherium copei.** Juv. Showing the deciduous fourth premolar in the immature skull. No. 521, in the Collection of the American Museum of Natural History.....Page 146.
- Fig. 5.—**Aceratherium occidentale.** A series of molars from the Lower Oreodon Beds, identical in character and measurement with Leidy's cotype of this species. Specimen No. 1107, in the Collection of the American Museum of Natural History.....Page 150.
- Fig. 6.—**Aceratherium occidentale.** The deciduous premolars in the calf *Aceratheres* skull, No. 534, in the Collection of the American Museum of Natural History.....Page 154.
- Fig. 7.—**Aceratherium occidentale.** A specimen from the Upper Oreodon Beds, showing the progressive development of the premolars, toward the *A. tridactylum* type. No. 1123, Collection of the American Museum of Natural History.....Page 154.
- Fig. 8.—**Aceratherium tridactylum.** Specimen No. 1122, belonging to a fragmentary skull in the Collection of the American Museum of Natural History. Page 159.
- Fig. 9.—**Aceratherium platycephalum.** Type Maxilla, No. 540, in the Collection of the American Museum of Natural History.....Page 140.
- Fig. 10.—**Aceratherium platycephalum.** Third and fourth premolars, showing a greater degree of wear. Cotype, No. 542, in the Collection of the American Museum of Natural History.....Page 142.



1. ACERATHERIUM TRIGONODUM. 2. ACERATHERIUM MITE. 3. ACERATHERIUM COPEI. 4. ACERATHERIUM COPEI JUV. 5. ACERATHERIUM OCCIDENTALE
 6. ACERATHERIUM OCCIDENTALE JUV. 7. ACERATHERIUM OCCIDENTALE 8. ACERATHERIUM TRIDACTYLUM 9. ACERATHERIUM PLATYCEPHALUM. 10. ACERATHERIUM PLATYCEPHALUM.
 All Figures Nat. Size.

PLATE XIV.

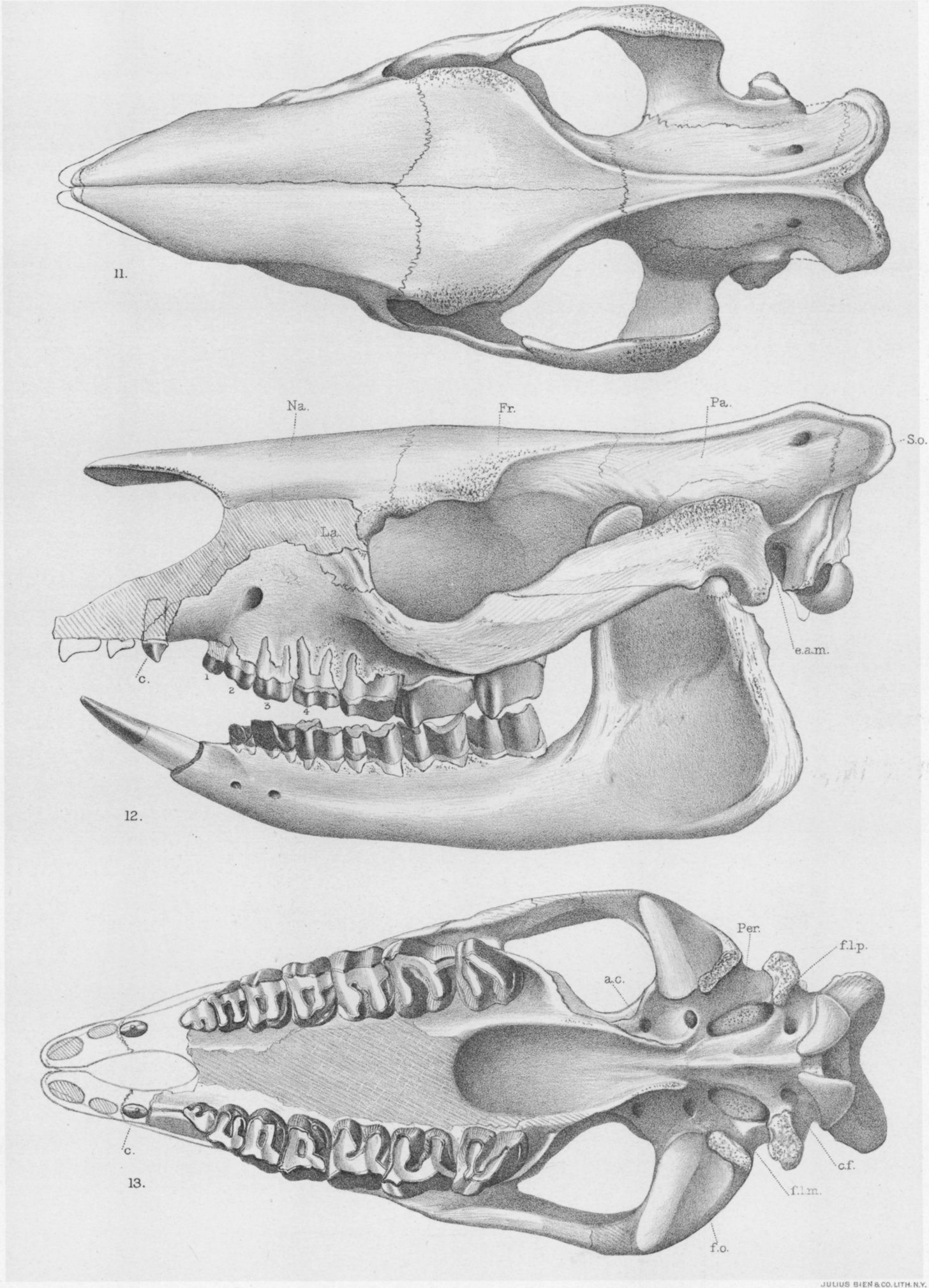
EXPLANATION OF PLATE XIV.



Leptaceratherium trigonodum.

One-third natural size.

Superior, lateral and inferior views of the Cotype skull, No. 529, in the Collection of the
American Museum of Natural History..... Page 132.



JULIUS BIEN & CO. LITH. N.Y.

ACERATHERIUM TRIGONODUM.

† Natural Size.

PLATE XV.

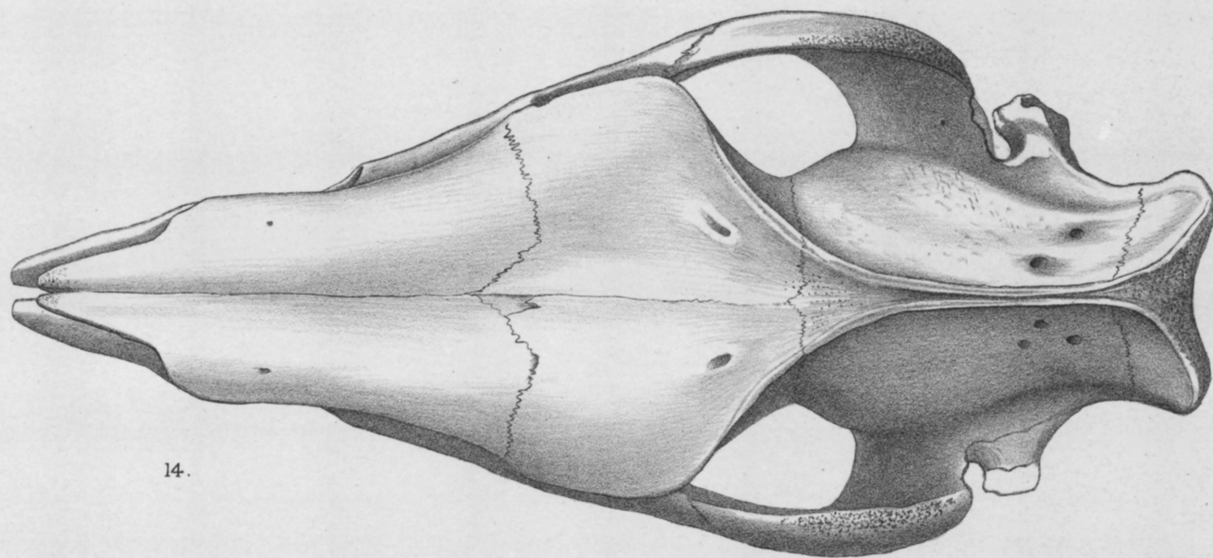
EXPLANATION OF PLATE XV.

Aceratherium copei.

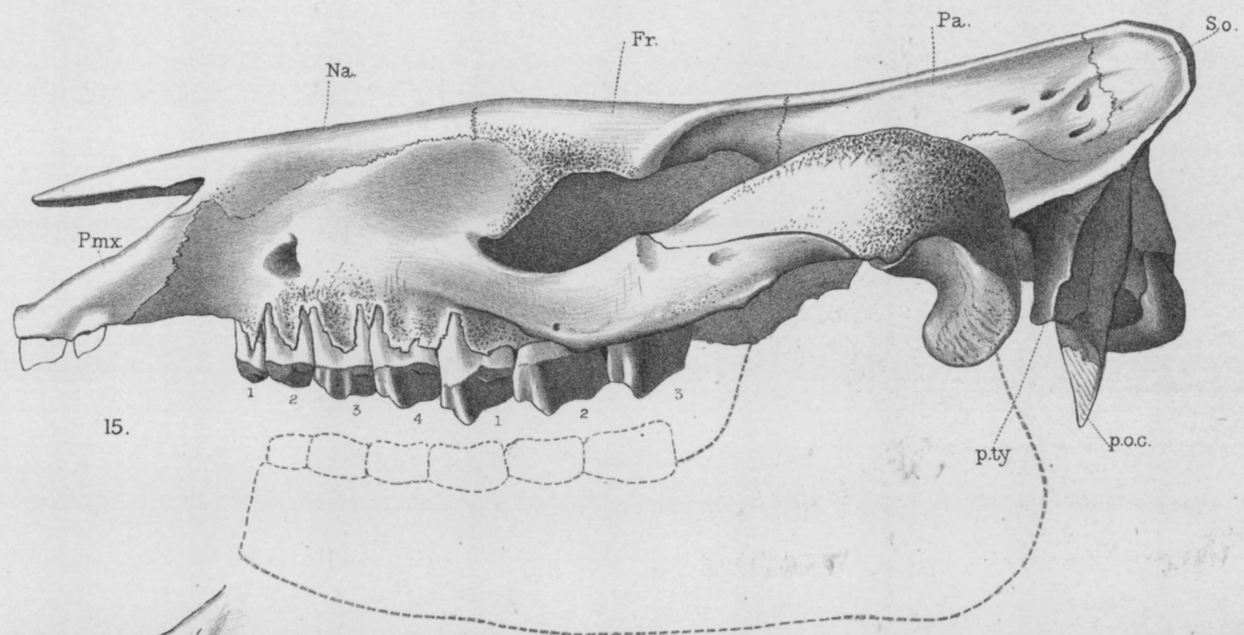
One-third natural size.

Figs. 14, 15, 17.—Superior, lateral and inferior views of the adult skull, No. 522, in the Collection of the American Museum of Natural History.....Page 146.

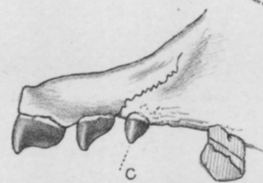
Fig. 16.—Premaxillary region of the immature skull, No. 521, showing the small superior canine tooth which is subsequently dropped or shed, and the permanent second and third incisors.....Page 146.



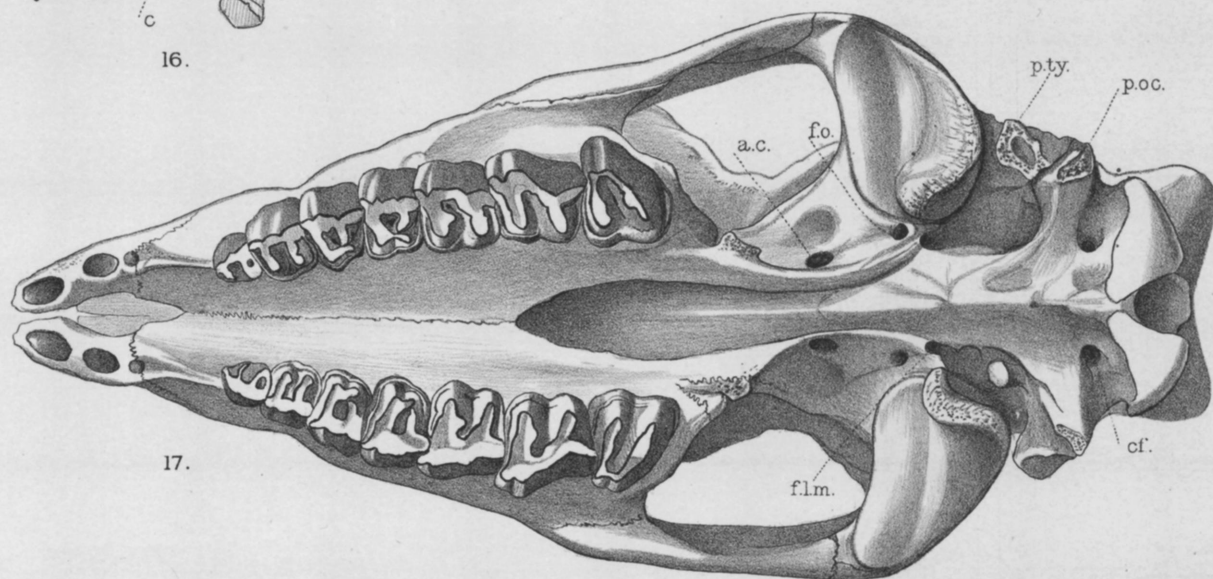
14.



15.



16.



17.

ACERATHERIUM COPEI.

† Natural Size.

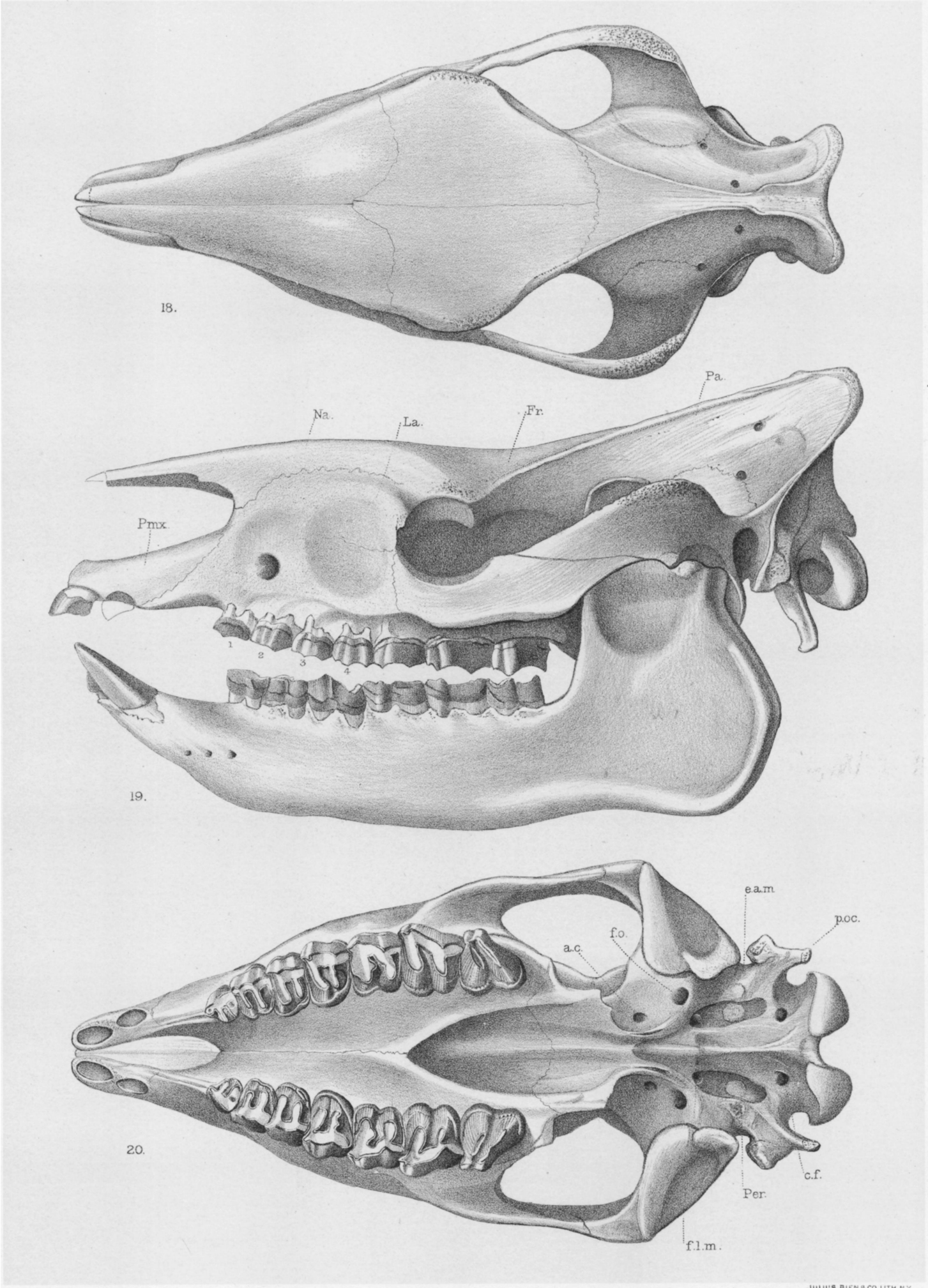
PLATE XVI.

EXPLANATION OF PLATE XVI.

Aceratherium occidentale.

One-third natural size.

Superior, lateral and inferior views of the adult skull. Composite drawing, combining the characters observed in a number of the skulls in the Collection of the American Museum of Natural History, representing a skull characteristic of the "Middle Oreodon level"Page 150.



ACERATHERIUM OCCIDENTALE

‡ Natural Size.

PLATE XVII.

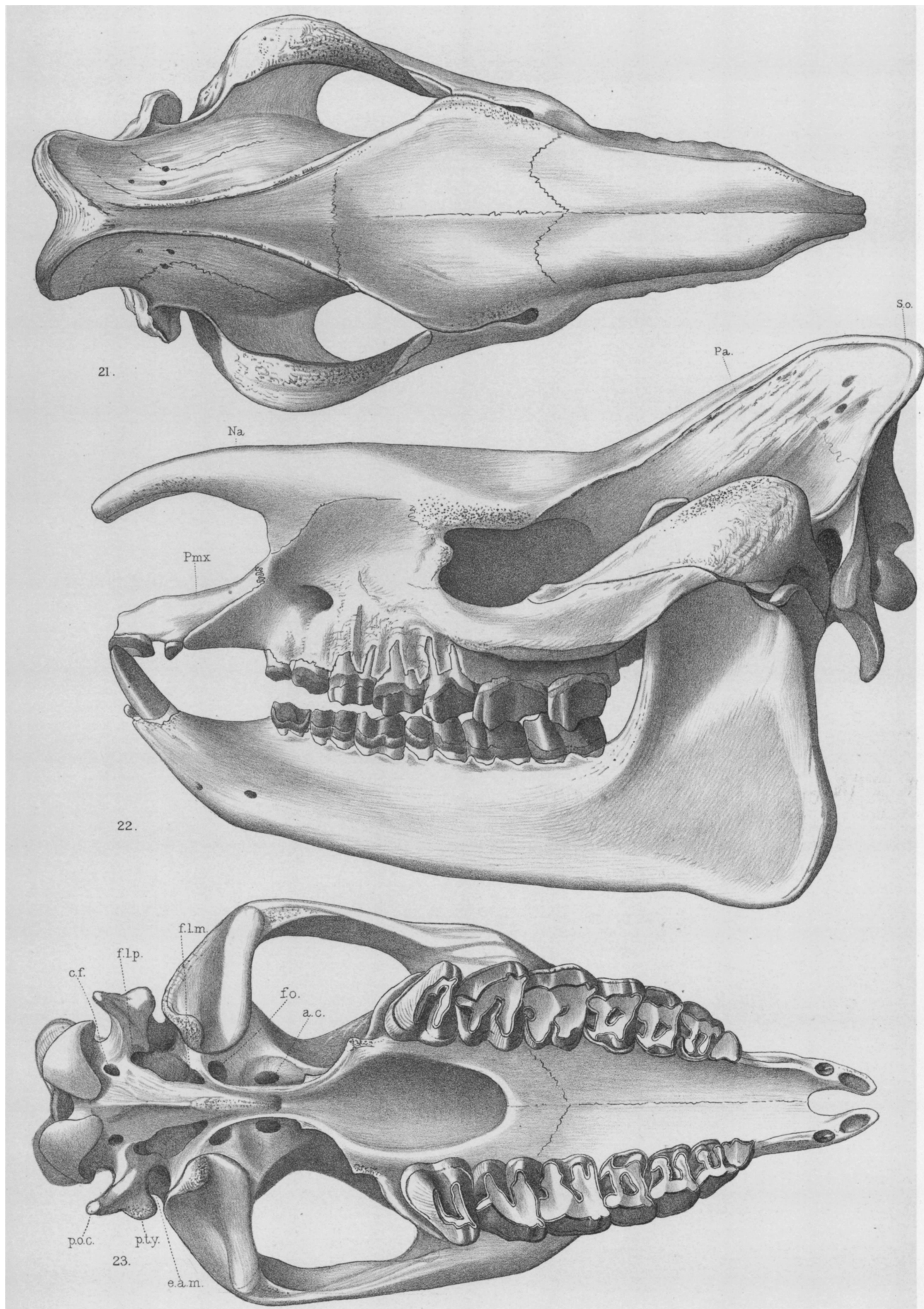
EXPLANATION OF PLATE XVII.

Aceratherium tridactylum.

One-third natural size.

Figs. 21 and 22.—Superior and lateral views of the Type skull, No. 538, in the Collection of the American Museum of Natural History..... Page 158.

Fig. 23.—Basal view of the skull, No. 541, in the Collection of the American Museum of Natural History..... Page 161.



ACERATHERIUM TRIDACTYLUM.

$\frac{1}{3}$ Natural Size.

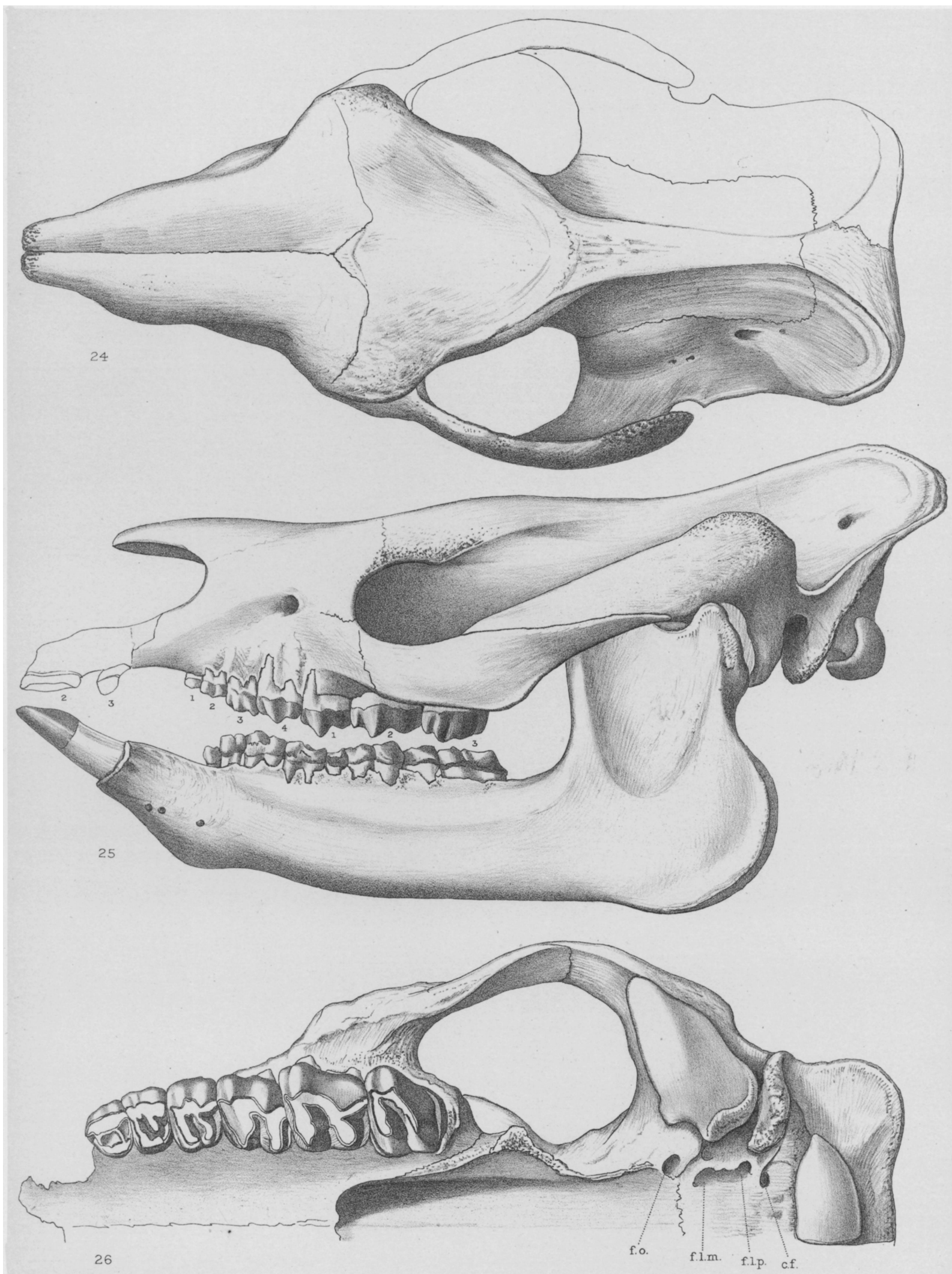
PLATE XVIII.

EXPLANATION OF PLATE XVIII.

Aceratherium platycephalum.

One-third natural size.

Superior, lateral and inferior views of the Cotype skull, No. 542, with the lower jaws of another specimen, No. 1444, in the Collection of the American Museum of Natural History. The figure is inaccurate in the too great foreshortening of the nasals and other parts in front of the orbits. The text figure (Fig. 41) is more accurate. Page 140.



ACERATHERIUM PLATYCEPHALUM.

† Natural Size.

PLATE XIX.

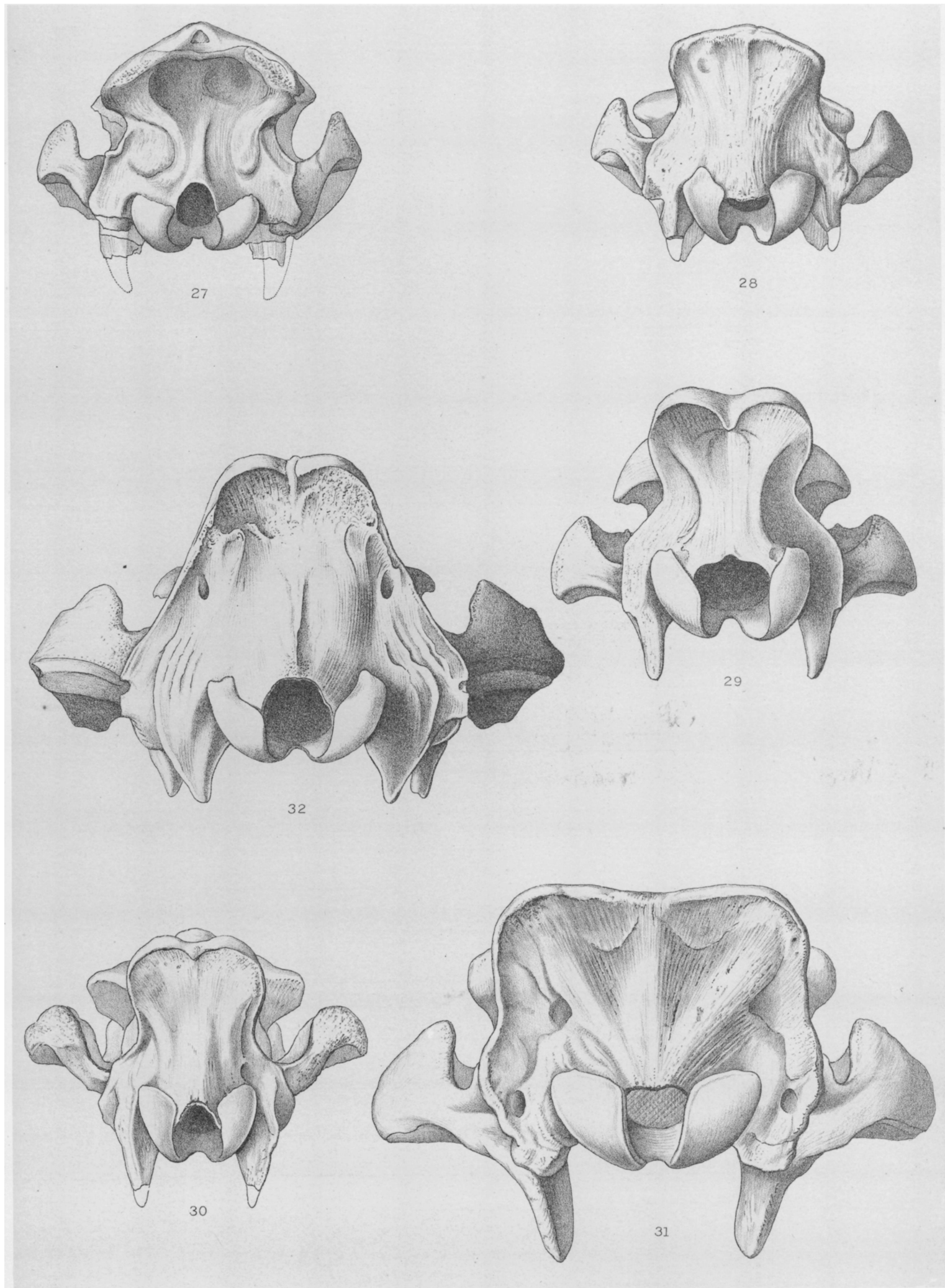
EXPLANATION OF PLATE XIX.

Occipital Region of the Skull.

One-third natural size.

All the originals are in the Collection of the American Museum of Natural History.

- Fig. 27.—**Aceratherium trigonodum.** Occiput of the skull, No. 529, figured in Plate XIV.....Page 135.
- Fig. 28.—**Aceratherium copei.** Occiput of the skull, No. 522, figured in Plate XV.
.....Page 149.
- Fig. 29.—**Aceratherium occidentale.** Occiput of the skull, No. 537.....Page 153.
- Fig. 30.—**Aceratherium tridactylum.** Occiput of the skull, No. 528, figured in Plate XVII.....Page 161.
- Fig. 31.—**Aceratherium platycephalum.** Occiput of the skull, No. 542, figured in Plate XIX.....Page 143.
- Fig. 32.—**Aceratherium (Aphelops) megalodum.** Occiput of Type skull in the Cope Collection of the American Museum of Natural History. From the Loup Fork or Upper Miocene Beds.



27. ACERATHERIUM TRIGONODUM. 28 ACERATHERIUM MITE. 29. ACERATHERIUM OCCIDENTALE.
30. ACERATHERIUM TRIDACTYLUM. 31. ACERATHERIUM PLATYCEPHALUM.
32 ACERATHERIUM MEGALODUM.

All Figures $\frac{1}{3}$ Nat. Size.

PLATE XX.

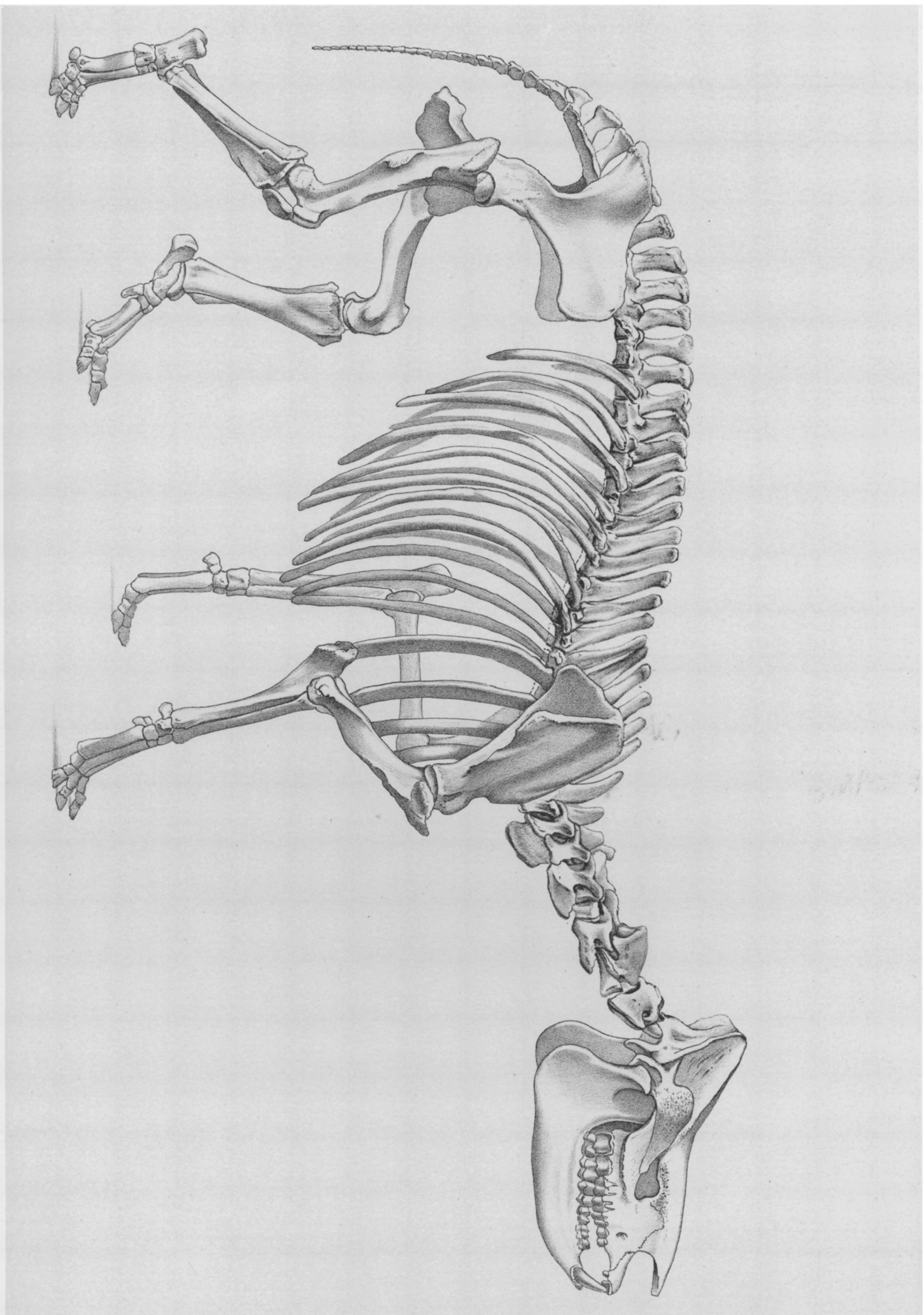
EXPLANATION OF PLATE XX.



Aceratherium tridactylum.

One-ninth natural size.

The mounted type skeleton, No. 538, in the Collection of the American Museum of
Natural History..... Page 159.



ACERATHERIUM TRIDACTYLUM.

§ Natural Size.

