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CONTRIBUTIONS FROM THE MUSEUM OF GEOLOGY AND ARCHÆOLOGY OF PRINCETON COLLEGE.

No. 1.

PALÆONTOLOGICAL REPORT

OF

The Princeton Scientific Expedition

OF 1877.

BY

HENRY F. OSBORN,
WM. B. SCOTT,
FRANCIS SPEIR, JR.

SEPTEMBER 1, 1878.

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1878.

PALÆONTOLOGICAL DIVISION.

PROF. JOSEPH KARGÈ,

ROLLIN H. LYNDE,

HENRY F. OSBORN,

JOTHAM POTTER,

WM. B. SCOTT,

FRANCIS SPEIR, JR.

To the Honorable the President and Board of Trustees of the College of New Jersey:

Gentlemen:

I have the honor to transmit herewith the Palæontological Report of the College Scientific Expedition of 1877.

The fossils collected by the Palæontological party, and deposited by the chief of the expedition in the Geological Museum, consisted of two sets, one numbering some two thousand specimens of fossil plants and insects from the tertiary beds of Central Colorado, the other of a considerable series of fossil vertebrates, mostly mammals, from the tertiary beds of Wyoming Territory, around Fort Bridger. This last collection has been studied and worked out with unabated zeal and diligence by the three post-graduate members of the Palæontological party, Messrs. H. Osborn, W. Scott, and F. Speir, who devoted most of the time of their course to this special work, with what success this Report will show.

It will be a source of gratification to the generous friends of the College, who furnished means for the Scientific Expedition of 1877, *that it not only enriched our Museum to so great an extent, but did more still by fostering in our College a thorough study of Palæontology, which could not have been undertaken without such means as these thus placed at the disposal of our students.*

The fossil insects and plants have been intrusted to the hands of the best specialists for determination. Dr. S. Scudder, of Cambridge, Mass., has kindly consented to revise the insects, Prof. G. L. Lequereux the plants.

Very Respectfully,

A. GUYOT,

Director of the E. M. Museum of Geology and Archæology.

PRINCETON, June 1, 1878.

SIR: We transmit herewith our report upon the Palæontological collections made by the Princeton party in the summer of 1877.

The following persons constituted the Palæontological division: ROLLIN H. LYNDE, HENRY F. OSBORN, JOTHAM POTTER, WM. B. SCOTT, FRANCIS SPEIR, Jr. The division remained in Colorado from the first of July until the first of August, when, under the direction of Professor Kargè, it left the main party, and passed the month of August in Wyoming, returning in the first part of September. The Colorado collections were mostly made in the (probable) Miocene beds near Florissant, and in the beds near the Garden of the Gods, variously referred to the *Dakota* and *Wealden* groups. In Wyoming, with Fort Bridger as a base of explorations, the division was wholly occupied in the Bridger series, camping successively on Smith's Fork, Henry's Fork, and Dry Creek, and exploring the beds adjacent.

It has been our endeavor, in confining our attention to the remains of vertebrated animals collected during the trip, not merely to catalogue the direct results, but, by the aid of fresh materials, to supplement the work of others. For, of the descriptions and data of the Bridger Eocene Fauna published up to the present time, we find that even those which have been most accurately prepared are lacking in important details; and that, owing to imperfect materials, large gaps yet remain in our knowledge of genera and species named and classed years ago. Although such supplementary work may appear, at first sight, tedious and ill-directed, we are confident that in the end it will prove of some value to science, and that it is therefore well worthy of our effort. While our field work did not extend beyond a region previously well explored, we obtained material by means of which we are able to add a number of new ossils to the Eocene Fauna of the Bridger group.

In the preparation of this report we have experienced much difficulty in assigning some of our specimens to their proper genera and species. For, while we have desired to respect the classifications made by others, we have in many cases found it impossible to do so, owing to uncharacteristic definition, which, without doubt, has been unavoidable. In all cases of uncertainty, we have adopted the classification which appeared to be the best established. This, in short, has proved the only available course.

The drawings have been executed with much care as to accuracy of proportion and outline. They are, with one exception, the work of a member of the party; and they are inserted simply to illustrate certain parts of the conte which would be unsatisfactory without reference to figures of the kind.

Now that the present work is ready for the press, we are very sensible th it must contain errors which, while they have escaped our notice, will be readi detected by eyes more experienced. These, we trust, will be excused, whe it is remembered that we are just entering a field which others have explore for years; and opening a work which Princeton, with her many other lin of study, has never hitherto attempted.

We take this opportunity to return our most hearty thanks to Gener Flint, to Judge and Dr. Carter, to Mr. Hamilton, and other officers an residents at Fort Bridger, who, by their good will and liberal assistance, contributed largely to our success. Our gratitude is also due to Professors Leidy and Cope for their generous aid, both in the way of advice and of material put in our hands for comparison.

The following pages do not embrace descriptions of the entire collections made by the Princeton party last summer. The valuable specimens of fossil plants and insects have passed into other hands.

Respectfully submitted,

HENRY F. OSBORN,
WM. B. SCOTT,
FRANCIS SPEIR, Jr.

Dr. Arnold Guyot,
Director of the E. M. Museum.

I.

ON THE SKULL OF THE EOCENE RHINOCEROS, ORTHOCYNODON, AND THE RELATION OF THIS GENUS TO OTHER MEMBERS OF THE GROUP.

W. B. SCOTT,
HENRY F. OSBORN.

PART I.—ORTHOCYNODON.

The skull of *Orthocynodon* was discovered in 1878 by one of the Princeton parties in the Bridger Beds of the Middle Eocene of Wyoming Territory. The exposure is what is known as the Washakie Basin of the Bitter Creek country. The beds were fully identified by the presence of *Palæosyops* and *Achænodon*, and by the fact that overlying them were numerous remains of the *Dinocerata*. Fragments of the appendicular skeleton were also obtained, but cannot be attributed to *Orthocynodon* with any certainty. An account of this animal was first given in the American Journal of Science and Arts, September, 1882.

Our conclusions, which are more fully given later in a discussion of the derivation of the Rhinoceros, are that *Orthocynodon*, showing relationship intermediate between *Hyrachyus* and *Amynodon*[1] of the Upper Eocene, is the earliest member of the Rhinoceros group thus far known. This relationship is indicated by all the principal characters of the teeth and skull. This genus differs from *Amynodon* principally in the canine teeth, which are erect instead of procumbent and in the pattern of the premolars. But the resemblances of these two genera to each other, and the characters in which they both differ from the *Hyracodontidæ*, on the one hand, and the *Rhinoceridæ*, on the other, justify our placing them in a new family, the *Amynodontidæ*.

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[1] We are indebted to Professor Marsh for allowing us to thoroughly examine the skull of *Amynodon* in his collection. The exposure of the mastoid portion of the periotic was a point of particular interest, which it was impossible to decide positively owing to the advanced age of the skull. The appearance of the bones, however, indicated a small exposure.

AMYNODONTIDÆ, FAM. NOV.

Rhinoceros-like animals; as far as yet known confined to the Middle and Upper Eocene; hornless; post-glenoid and post-tympanic processes do not unite below the auditory meatus; a small exposure of the mastoid portion of the periotic on the side of the skull; no post-cotyloid process on the mandible; canines and incisors present and functional in both jaws; lateral incisors usually absent; pattern of the first three upper premolars unlike the molars; pattern of the molars like that of the Rhinoceros, but with the transverse crests simple; probably four toes in front, three behind.

Genera.

AMYNODON,[1] Marsh. Generic characters: lower canines procumbent, incisors two on each side above and below, the pattern of the premolars throughout unlike that of the molars.

ORTHOCYNODON,[2] Scott and Osborn. Generic characters: lower canines erect, the third upper premolar has a low posterior crest, two incisors on each side (the lateral apparently absent), the fourth upper premolar has distinctly the molar pattern of anterior and posterior crests.

Orthocynodon antiquus. Specific characters: accessory ridges on first upper molars only, posterior crests on third upper premolars low, canines trihedral and slightly recurved,

THE SKULL OF ORTHOCYNODON.

The skull (Plate V) in the Princeton collection lacks the forward portions of the nasal and maxillary bones, so that the characters of the nasals can only be conjectured; all the upper teeth anterior to the third premolar are also wanting. A mass of matrix lying over the orbit could not be removed, so that this portion, although figured, is not positively known, nor is the position of the lachrymals ascertained. The upper portion of the occiput and the basal region of the skull are also somewhat imperfectly preserved. The posterior portion of the jaw, including the angle and condyle, belongs to the right side of the skull, while the symphysial portion belongs to the left. The forward portion of the skull is restored, after a careful study of the worn surfaces of the lower teeth and of the portions of the nasal and maxillary bones which remain.

The general character of the skull is slender and elongate

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[1] American Journal of Science and Arts, 3d series, vol. xiv. p. 251.

[2] Ibid., vol. xxiv. p. 223. Owing to a more perfect exposure of the skull we can correct some errors in our first statement.

with a light zygoma, extensive temporal fossa and quite a prominent sagittal crest. At first sight the skull is wholly different from that of the Rhinoceros, but a closer inspection shows all the prominent rhinocerotic features in their incipient stages. In fact, *Orthocynodon* differs from *Rhinocerus* in much the same manner that all the other Eocene types which have persisted differ from their descendants. We find a low instead of a high occiput, a sagittal crest instead of a flat cranium, a slender mandibular ramus and prominent canines.

More in detail, the *frontals* are short, while the *parietals* are elongated. The brain-case indicates rather a long narrow brain. The temporal fossa is not as deep as in *Palæosyops*, but is extensive; posteriorly it is bounded by a slight ridge at the sides of the occiput. The sagittal crest is quite high and thin; it is

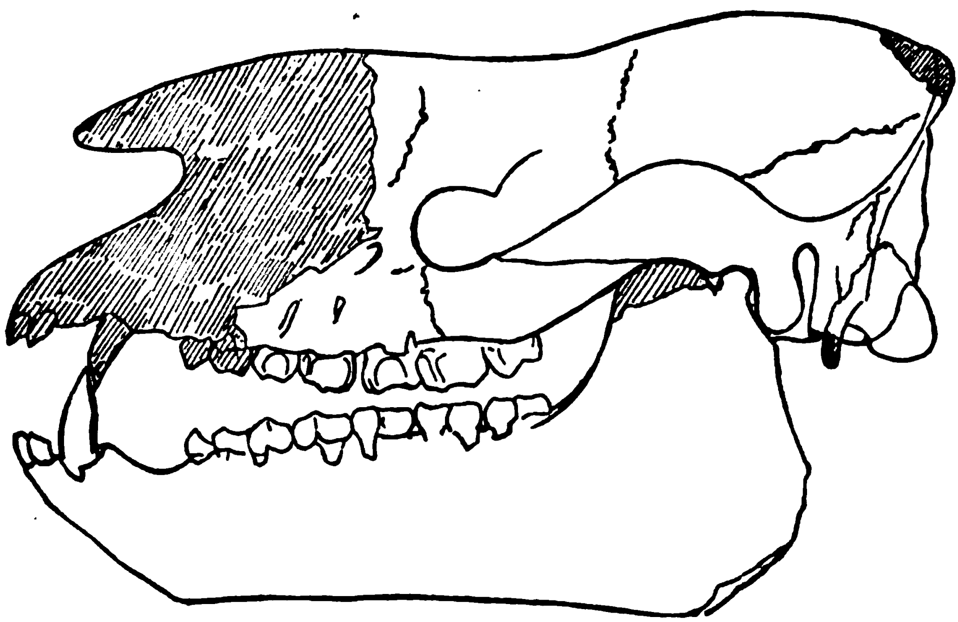

Fig. 1.—Restoration of Orthocynodon. (One fifth natural size.)

extended backwards upon the *supra-occipital* so as slightly to overhang the occiput when the skull is in a horizontal position. Forwards the crest disappears in the well-rounded snout, without passing into supra-orbital ridges. Above the orbits is the fronto-nasal suture. The skull has an oval section at this portion, and the nasals begin to rise as in the modern Rhinoceros. The orbit is small, and there is probably a very slight post-orbital process; the anterior edge of the orbit is over the second molar. The limits of the *lachrymals* cannot be ascertained. They undoubtedly had a small exposure upon the face. The infra-orbital foramen is slightly anterior to the orbit.

The *maxillaries* slope forwards, indicating a narrow upper jaw; the horizontal plate as well as the palatine bones are wanting. The *malars* extend to the inferior border of the orbit, forming a considerably smaller portion of the face than in the Rhinoceros. The zygomatic arch is slender as in *Aceratherium*, lacking the robust character which it has in *Palæosyops*. The external surface projects considerably beneath the orbit; posterior to this the arch is slender and narrow in vertical section, not projecting widely from the skull. The malar-squamosal articulation is not very close. The zygomatic border passes downwards into the heavy post-glenoid process. This process is deep and quite broad, and placed directly behind the condyle of the jaw. This is quite different from its light character and internal position in *Rhinocerus*. There is no pre-glenoid border. Behind this process is the wide external auditory meatus; the distinctive character of this portion of the skull is that the post-glenoid and post-tympanic processes are quite widely separated below. Behind the auditory meatus is a triangular surface composed of portions of the squamosal, the periotic and the ex-occipital bones; this surface is divided from the temporal fossa by a low ridge, and it slopes away posteriorly into the occiput. This surface offers a great contrast to the compressed space between the occiput and the temporal fossa in the Rhinoceros. The exposure of the mastoid is faintly outlined in the restoration (Fig. 1). It cannot be traced throughout with certainty owing to the close forward union with the squamosal. It is, however, quite as clear as in many of our specimens of *Hyracodon*. The resemblance of this portion of the skull to *Hyrachyus* is remarkably close. The *squamosal* ascends well upwards and backwards, forming the posterior portion of the temporal fossa. The occiput is quite narrow above and broad below; the *supra-occipital* is partially broken. The limits of the *ex-occipitals* are clearly defined; they have similar relations to those in *Rhinocerus*, sending down a rather slender par-occipital process which has a long union with the post-tympanic. The occipital condyles are very convex and projecting; they are largest in vertical diameter and directed obliquely downwards and backwards; their lateral extension is not very great. The basi-cranial region is not well defined, and it cannot be ascertained whether there was an alisphenoid canal.

The *lower jaw* has the typical ungulate character. The chin is shallow and sloping; the ramus is not very deep; the angle is very broad and flat, with a much elevated condyle. The symphysis is long and oblique. There are apparently two mental foramina placed beneath the canine-premolar diastema. The border of the jaw at the diastema is thin. The incisor alveolus is wanting, but the teeth are held *in situ* by the matrix; they have a nearly erect position. Marking the posterior edge of the symphysis below is a slight downward swelling. Behind the molars the superior border rises rapidly, indicating a light coronoid process. The condyle is broad and convex; it has no post-cotyloid process. Beneath it the posterior border of the jaw is recurved. The angle of the jaw is rounded and comparatively thin, wholly lacking the heavy rugose character of the angle in *Rhinocerus*.

Measurements of Skull.

	M.
Total length of skull estimated, about 17 inches	.44
Height of skull, including lower jaw	.23
Width of skull just below the orbit, including the malars, approximate..............	.16
Length of zygomatic arch from posterior surface of post glenoid process to malar maxillary suture..........................	.17
Length of mandibular ramus, approximate.	.36
Depth of " " below root of first molar	.065
Depth of ramus from top of condyle to lower border of angle, approximate	175
Length of mandibular symphysis, approximate	.09

Other measurements may be taken from Plate V, which is executed accurately upon a half scale.

DENTITION OF ORTHOCYNODON.

LOWER JAW. *Incisors.* Of the lower incisors our specimen has three in position, the two median and a lateral of one side. The alveolus of the jaw is all crumbled and broken so that the number of the incisor teeth cannot be definitely determined. It certainly was not less than two, and *may* have been three, as there is an abundance of space for an additional tooth between the second incisor and the canine, the symphysis being considerably broader than in *Amynodon*, where the canines and incisors are closely crowded together.

The incisors are represented in Plate V, Figs. 1 and 4. In the former figure the left median and the front face of the right median are both seen; in Fig. 4 the summits of the two median incisors are seen.

The median incisor is the larger of the two; in shape its crown is quite similar to that of the corresponding tooth in the Tapir, but is smaller and more acute. The upper edge is like an inverted V, and not a straight line as in the Tapir. From the apex, which is truncated by attrition, a low ridge runs obliquely down the posterior face of the crown. The cingulum is very feebly marked in the anterior surface of the tooth, but is quite strong in its lateral and posterior surfaces.

The second incisor, which is too much broken to admit of accurate description, is separated from the median one by a narrow space. It has a somewhat everted conical crown. Both teeth have long, straight and simple fangs.

The lower incisors are not at all like those of *Rhinocerus* in either position or shape, being small, acute and nearly erect. Even in *Amynodon* the incisors have begun to be very much more procumbent.

The *Canine* is a very large tooth; it stands erect and is even slightly recurved, one of the most striking differences between this genus and *Amynodon*, which has the "lower canines placed nearly horizontal."[1] In the specimen before us the canine is long, pointed and somewhat everted, so that it stands somewhat outside the line of the molar series. In shape a section of the crown is somewhat trihedral, with a flat posterior surface; the other surfaces are slightly rounded. The upper portion of the posterior face is worn bare of its enamel by the action of the upper canines.

The fang is stout, sub-cylindrical and strongly recurved, running down into the jaw for nearly the entire length of the symphysis.

In *Amynodon* the canine has assumed a shape more characteristic of the Rhinoceros type, in being more compressed and having trenchant edges, while in *Orthocynodon* the only departure from the Lophiodont pattern is in the increase in size of the lower canine.

Premolars. These teeth (Fig. 3), four in number, form an unbroken series as in *Hyrachyus*. The first premolar is separated from the canine by a long diastema, and is inserted by two fangs of nearly equal size. Seen from the outer side, the tooth has a conical crown obscurely divided into two lobes by a faint ridge running obliquely down its outer face. The crown is compressed and narrow and has its anterior and posterior edges sharp and trenchant. Internally the two lobes are more apparent, the anterior fossa being very shallow and the posterior quite distinct. The very obscure cingulum is present only in the inner face. The tooth is very like the first milk-molar of *Rhinocerus indicus*.

The second premolar is much larger than the first, and, while presenting no new elements, approximates more the type of the molars. The groove separating the external lobes is more marked, the median internal crest very much more decided, and the anterior and posterior edges of the crown are raised into rudimentary crests. As a whole, the tooth is very similar in construction to the corresponding tooth of *Hyrachyus*.

The third and fourth premolars show a closer and closer approximation to the molar pattern; the lobes being more clearly defined, and the posterior lobe becoming larger than the anterior. In the third premolar the anterior crest is more feeble than in the molars, but in the fourth (the crown of this tooth is somewhat broken) there seems to be no deviation from the molar type.

The *Molars*, of which the third is missing from our specimen, need no especial description, being entirely like those of *Aceratherium*, *Hyracodon* and *Rhinocerus*. The only point that deserves mention is the comparatively small size of the anterior

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[1] Marsh, Amer. Jour. Sci. and Arts, 3d ser., vol. xiv. p. 251.

attention to the fact that in this line of Perissodactyls a further series of modifications "consists of a successive complication of the transverse crests." In the American species of *Aceratherium* this complication goes no further than the formation of a bulge (ante-crochet, Lydekker) from the anterior crest into the median valley in the first and second molars. In the European and Indian species this bulge is sometimes present; more commonly a corresponding projection from the *posterior* transverse crest (crochet, Lydekker) into the median valley is found in all the molars and some of the premolars, as is the case in the living species of Sumatra, India and Africa. In *Orthocynodon* the projection from the anterior crest is present only in the first molar, the crests of the other two being perfectly simple.

Another complication found in the recent forms is seen in the great elevation of the cingulum on the posterior face of the molars so as to form accessory crests, and when the tooth is somewhat worn down these are seen to enclose small fossæ. This is seen in a less degree in *Aceratherium* and *Hyracodon*, and the beginnings of it in *Orthocynodon*, in which form the cingulum of the first molar shows a prominence at the hinder surface of the crown. This is not seen in the other molars. Thus in all respects the first molar shows a closer approximation to the more recent and complex kinds of teeth than do the others.

The second molar is, as is usual in this group, much the largest of the series; it is the typical Rhinoceros molar without any accessory complications.

The third molar shows some interesting peculiarities. Prof. Cope[1] has noted that in *Aceratherium* and the more recent forms the posterior crest is confluent with the external wall of the tooth, while in *Hyracodon* the posterior crest is distinct from the outer wall, which, as in the Lophiodonts, is continued well back of the posterior crest. In *Orthocynodon* there is, as we should naturally expect, a more primitive condition even than in *Hyracodon*; the outer wall is produced much beyond the posterior crest, so that a wide and deep fossa is enclosed between the two. At the posterior angle of the cutting edge the wall and the crest are connate; from this point the former slopes upwards and backwards. (Plate V, Fig. 2).

The form of the crown is thus a step towards *Hyrachyus* as compared with the Miocene forms.

The molar teeth came into use very much as in *Rhinocerus*. The last molar shows no wear at all, while the other two, especially the first, are very much worn down.

Regarded as a whole, the dentition of *Orthocynodon* is strictly intermediate between the Lophiodonts of the Eocene and the Aceratheria and Hyracodonts of the Miocene, though, curiously

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[1] Loc. cit.

enough, it shows a greater specialization of the premolars than is seen in *Amynodon.*

Measurements.

Lower Jaw.	M.
Transverse diameter of median incisor	.009
Antero-posterior " " " "	.011
Transverse " " 2d "	.008
Distance between 1st and 2d incisors	.006
" " 2d incisor and canine	.009
(There was thus abundance of space for a third incisor.)	
Vertical height of crown of *canine*	.035
Transverse diameter of crown of canine at base (approx.)	.020
Fore and aft diam. of crown of canine at base	.015
Length of worn surface, measured from apex	013
Length of diastema between canine and premolars	.040
Length of entire molar series (without last molar)	.165
Length of premolar series	.080
Fore and aft diameter of 1st *premolar*	.013
Transverse " " " "	.009
Fore and aft " " 2d "	.019
Transverse diameter of 2d *premolar*	.015
Fore and aft " " 3d "	.023
Transverse " " " "	
Fore and aft " " 4th "	.029
Transverse " " " "	.017
Fore and aft " " 1st *molar*	.037
Transverse " " " "	.024
Fore and aft " " 2d "	.044
Transverse " " " "	

Upper Jaw.	M.
Fore and aft diameter of 3d *premolar*	.019
" " " " " 4th "	.022
Transverse " " " "	.033
Length of true molar series	.104
Fore and aft diameter of 1st *molar*	.037
Transverse " " " "	.037
Fore and aft " " 2d "	.045
Transverse " " " "	.037
Fore and aft " " 3d "	.028
Transverse " " " "	.030

PART II.—DERIVATION OF THE RHINOCEROS GROUP.

The Rhinoceros group is at present represented by three genera, perhaps four, which are confined to the Oriental and Ethiopian regions. Formerly, however, it had a much wider range and was very much richer in genera and species. Remains of various members of the series have been found all over Europe, Asia and North America, and the origin of this line has been pushed further and further back in time by successive discoveries. The earliest members of the series have been found in the Upper and Middle Eocene of Utah and Wyoming, the former deposits yielding *Amynodon*, and the latter *Orthocynodon.*

The origin of the Rhinoceros line from Eocene Tapiroids was first suggested by Prof. Marsh,[1] and has been abundantly confirmed by subsequent investigations. Gaudry's[2] view that *Palæotherium* is to be regarded as the ancestral type is beset with many difficulties, and is sufficiently disposed of by the fact that at, or even before, the time when *Palæotherium* appeared in Europe unmistakable Rhinoceroses were already living in America.

In the Lophiodont genus *Hyrachyus* of the Eocene we have the common ancestor of no less than four distinct lines of Perissodactyls, two of which, the Rhinoceros and Tapir, are still

[1] Introd. and Success. of Vert. Life in America, Am. Journ. Sci. and Arts, 3d ser., vol. xiv. p. 361.

[2] Les Enchaînements du Monde Animal, ch. iii.

living, and two, the *Hyracodon* and *Diceratherium* lines, are extinct. The discovery of *Orthocynodon* and *Desmatotherium*[1] throws a great deal of light upon the relationships of these various forms, and it is to be hoped that future discoveries will clear them up perfectly.

THE RHINOCEROS SERIES.

The first steps of the change from *Hyrachyus* towards *Rhinocerus* may be inferred from a careful comparison of *Hyracodon*, *Amynodon* and *Orthocynodon*, thus determining what features are common to the three. In this way we can in a measure reconstruct the common ancestor of these genera, which came one step further down than *Hyrachyus*.

The first change seems to have been the transformation of the molar teeth from the Lophiodont to the Rhinoceros type by the reduction of the antero-external lobe and greater obliquity of the transverse crests in the upper molars. In the lower molars the crests became more curved, less directly transverse and more closely united at their outer edges, while at the same time the descending ridge from the anterior crest, so well shown in some species of *Hyrachyus*, became still further developed, giving the characteristic double crescentoid pattern of the Rhinoceros molar. A worn molar of *Hyrachyus* shows the essential unity of the two patterns very distinctly.

It is also possible that in this hypothetical form the premolars underwent preliminary changes much as in *Desmatotherium*, but from the uncertainty as to the exact form of these teeth in *Amynodon* this cannot be stated definitely. In other respects the features common to the three genera under discussion are those possessed also by *Hyrachyus*, namely, (1) the presence of canine and incisor teeth in both jaws; (2) the extension of the external wall of the last upper molar beyond the posterior transverse crest;[2] (3) the exposure of the periotic bone on the surface of the skull; (4) the sagittal crest; (5) the transverse extension of the post-glenoid process; (6) the wide separation of the post-glenoid and post-tympanic processes; (7) the absence of a post-cotyloid process on the mandible; (8) the absence of any special thickening of the edge of the ascending mandibular ramus.

All of these characters must be supposed to be present in our hypothetical genus, and furthermore it almost certainly had four digits in the manus and three in the pes. From this point the two lines diverge, the *Amynodontidæ* passing to the *Aceratheria* of the Miocene, and the other line, possibly through *Triplopus*, to the Hyracodonts of the same formation.

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[1] See fourth paper of this Bulletin.

[2] See Cope, loc. cit. p. 234.

SKULL. The *Amynodontidæ* retain many Lophiodont characters, deviating markedly from the Rhinoceros type. Besides the points of resemblance to *Hyrachyus* already mentioned there remain other features of importance. The skull is long and narrow; the face is especially long as compared with that of *Aceratherium*. In the latter the edge of the orbit is directly over the middle of the first molar; in *Orthocynodon* it is over the middle of the second molar, a considerable difference at that point. Altogether the face, as nearly as we can judge from our specimen, forms very nearly half the length of the skull. The posterior part of the cranium projects proportionately further beyond the root of the zygomatic process, so that on the whole the skull is both longer and narrower relatively than in the *Rhinoceridæ*. The long and high sagittal crest is another Lophiodont feature that has been progressively obliterated as the line approaches the more modern forms. In *Aceratherium* the crest is much shorter, the broad surface of the skull extending well over the temporal fossæ. In *Aphelops* the crest is still further reduced, and through its entire length is divided into two ridges by a narrow intervening space. In the modern forms there is no sagittal crest at all, the whole upper surface of the head being very broad.

Another progressive change in the shape of the skull is seen in the rise of the occipital and parietal regions above the frontal. In *Orthocynodon* the upper line of the skull is not very far from straight, the sagittal crest curves slightly upwards from the level of the frontals, giving the cranium a shape very like that of *Hyrachyus*. In *Amynodon* the shape is more like that of the Tapir, while in *Aceratherium* there is a decided rise in the parietal region; a feature which is much plainer in *Aphelops*, and still more so in *Rhinocerus*.

One of the most characteristic differences between the Lophiodont and Rhinoceros types of skulls is the presence of the periotic on the surface in the former, and its absence from the surface in the latter. This bone is plainly visible in the side wall of the skull of *Orthocynodon*; it is probably present also in *Amynodon*. Prof. Cope[1] has also demonstrated its presence in *Hyracodon*. In correspondence with this arrangement we find in these three genera that this portion of the skull is very like that of *Hyrachyus*, being rather broad and triangular, while in *Aceratherium* and more recent genera the disappearance of the periotic from the surface is accompanied by a narrowing of this region into a mere ridge.

Another series of changes in the Rhinoceros skull is one emphasized by Prof. Cope in the pamphlet already quoted; namely, the relations between the post-glenoid and post-tympanic pro-

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[1] Loc. cit.

cesses of the squamosal. In the Lophiodonts and Tapirs these processes are widely separated, leaving the auditory meatus open below; a state of things which we also find in the Eocene *Amynodontidæ*. In *Aceratherium* the two processes approach each other, and in one of our specimens from Dakota are almost in contact. In *Aphelops* they touch each other, and in *Rhinocerus* they are co-ossified. *Ceratorhinus* and *Atelodus*, which are persistent Miocene genera, have the meatus still open. *Hyracodon* agrees with the other Miocene types in having these processes widely separated.

Other progressive modifications, as the change of the occipital condyles from projecting to sessile, the conversion of the broad and transversely directed post-glenoid process into a styliform shape, the appearance and increase of the post-cotyloid process, the thickening of the posterior edge of the ascending mandibular ramus, might be followed out in the same way, each one gradually leading up to the modern forms, in all of which respects *Orthocynodon* represents the first stage.

The BRAIN likewise indicates a continual advance, at least in size. In *Hyrachyus* there was quite a large brain for an Eocene mammal. The hemispheres were well developed and rounded, though little convoluted (as far as can be judged from a cranial cast); the olfactory lobes were large, and the cerebellum was lodged in a very distinct fossa. Of the details of the brain in *Orthocynodon* we know nothing, but judging from the general shape of the cranium, it appears to have been somewhat longer and narrower than in the Lophiodonts. Compared with the Eocene Rhinoceroses, *Aceratherium* had a much higher type of brain. The hemispheres are much larger, both in proportion to the skull and to the cerebellum; they are well convoluted, broad, rounded and somewhat depressed, and seem to have slightly overlapped the cerebellum. The olfactory lobes are considerably reduced in size. This brain is not unlike that of the modern species.

DENTITION. In the dentition the steps of progressive modification are very clearly seen. In *Orthocynodon* the only change from the Lophiodonts, besides the transformation of the molar teeth, is the enlargement of the lower canines and perhaps the loss of one pair of lower incisors. In *Amynodon* the canines are procumbent and compressed, and, "taken in connection with the rest of the anterior dentition, they prove conclusively that the large lower teeth, usually regarded as incisors in *Aceratherium* and many other members of the Rhinoceros family, are really canines" (Marsh[1]). This view of the homologies of these teeth is completely confirmed by their position in the Bridger genus, which is like that of all the Eocene Tapiroids. Their compressed

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[1] Am. Journ. Sci. and Arts, 3d ser., vol. xiv. p. 252.

shape and procumbent position in *Amynodon* give us the second step towards the Rhinoceros form of dentition. The loss of opposition consequent upon this procumbency of the lower teeth must be regarded as the cause of the atrophy of the upper canines. A similar process may be observed in the Tapir, where the opposition of the slightly procumbent lower canine has caused a great development of the upper lateral incisor. In consequence of this arrangement the upper canine and lower lateral incisor have both experienced a great reduction in size.

The increase in size of the upper incisor in *Aceratherium* and the modern forms seems to be due to the opposition of the lower canines. In the Eocene forms this process had scarcely begun, and so we see no especial modifications of these teeth in the *Amynodontidæ*.

THE SKELETON. The clear indications of advancing differentiation which are thus afforded by the skull, the brain and the dentition may be further extended and confirmed by a study of the skeleton.

In part this has already been done by Prof. Cope, but the comparison may be somewhat further extended.

Of the skeleton of *Orthocynodon* we know nothing with certainty, but that of *Aceratherium* still retains many features of its Lophiodont ancestry which are of much interest. Both this form and its Upper Eocene predecessor, *Amynodon*, had four digits in the manus and three in the pes. In the European species of *Aceratherium* the fifth digit is extremely small and functionless, evidently about to disappear. The whole skeleton in this genus is lighter, smaller and less specialized than in any of the living genera. The neck is longer and less massive; the axis has a particularly long centrum, its neural spine is lighter, in correspondence with the less massive head, and, as in the Lophiodonts, the spine is produced more backwards than forwards. Vertebræ of the other regions bear out the same conclusion. The limbs show similar relations, the bones being more slender and without that great development of the various processes which gives the bones of modern Rhinoceroses their characteristic appearance. The humerus and fore-arm bones are much stouter than in *Hyrachyus*, much more slender than in living forms. The carpus was expanded laterally, but was of a less antero-posterior diameter than in the Rhinoceros.

The metapodial bones of the Eocene Tapiroids are of two types: those of the *Chalicotheridæ* are short and stout, while the *Lophiodontidæ* have them long and slender. *Aceratherium* has these bones of the Lophiodont type, but they have become much heavier, and yet not so stout as in *Aphelops*, *Ceratorhinus* or *Rhinocerus*. There is less difference in size between the median and lateral metapodials than in these genera, and as a whole the foot is rather long and narrow. The astragalus of *Acera-*

therium is characteristically Rhinoceros-like, but it has a somewhat longer neck and a smaller facet for the cuboid.

As a whole, then, the skeleton of *Aceratherium* may be said to be intermediate between that of the Lophiodonts and that of the Rhinoceroses, though plainly with closer affinities to the latter.

It seems, therefore, that the derivation of the Rhinoceros line from Lophiodont forms, as first suggested by Prof. Marsh, may be regarded as established; and further, that, according to all present evidence, the group originated in North America. The earliest known European members of the series are the Miocene species of *Aceratherium*, which seem to have migrated from America, and there to have given rise to the horned genera. The only horned Rhinoceroses which have so far been found in America belong to the peculiar genus *Diceratherium*. It is possible that the genus *Aphelops* also migrated to the Old World, and was there ancestral to the horned types; but the evidence so far obtained goes rather to show that *Aphelops* was not in this line, but that the loss of the fifth digit of the manus took place independently in Europe and America, occurring in the former continent simultaneously with the development of dermal horns, and so giving rise to the genus *Ceratorhinus*. This genus has the auditory meatus open below, and has a type of molar teeth but little more complex than those of *Aceratherium*.

From *Ceratorhinus* were probably derived, as suggested by Prof. Cope, the two other living genera, *Rhinocerus* and *Atelodus:* the former by the closure and co-ossification of the auditory meatus and the development of a more complex type of molars; the latter by the loss of all canines and incisors. It seems likely that the development of the second horn in *Ceratorhinus* took place subsequent to the branching off of the genus *Rhinocerus*.

Atelodus appeared in the Upper Miocene of Greece, whence so much of the fauna of modern Africa was derived. *Rhinocerus* appears for the first time in the Upper Miocene of India, and still persists there. Prof. Cope[1] has described a new genus of Loup Fork hornless Rhinoceroses, which he calls *Peraceras*, and which he regards as the ancestral type of the African *Atelodus*. But it seems to us that his former view, quoted above, is the more probable one. *Peraceras* resembles *Atelodus* in the absence of all canines and incisors, but it was hornless and had the post-glenoid and post-tympanic processes in contact though not co-ossified. Then contemporary with, or perhaps even anterior to, this hornless form was the *A. pachygnathus* of Greece with both horns already developed.

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[1] Am. Naturalist, 1880, p. 540.

post-glenoid process, the exposure of the periotic on the surface of the skull, and the absence of any post-cotyloid process, as well as the shape of the mandible and the presence of a full set of canine and incisor teeth in both jaws, are all very strong evidences of the Lophiodont ancestry. While the molars and premolars are of the same pattern, the construction of the upper molars, and especially of the last one, reminds one strongly of the Eocene progenitors. Even the accessory ridge, which in *Hyracodon* projects from the outer wall of the tooth into the median valley, may be seen in some species of *Hyrachyus*.

When we come to examine the skeleton of the trunk and limbs we find that here the Rhinoceros characteristics are less distinct than in the skull and dentition, while the Lophiodont affinities are very clearly observable, and in addition there are a number of peculiarities not to be met with in either of the groups mentioned.

The neck is very slender and elongate; the cervical vertebræ are strongly opisthocœlous, and those behind the axis have broad flat zygapophyses without neural spines. The transverse processes were perforated. The length and flexibility of the neck is one of the strongest contrasts between *Hyracodon* and the Rhinoceroses; it is even considerably longer than in *Hyrachyus*. The thoracic vertebræ are also opisthocœlous, with deep, rounded, rib facets, and long, light and compressed neural spines. There is a lightness of structure about them very different from the heavy, solid vertebræ of the Rhinoceroses, and more like those of the Lophiodonts. The lumbar vertebræ seem to have been six or seven in number. The anterior ones are compressed and the posterior depressed; the spines are short and rather light. The sacrum is not unlike that of the Rhinoceros, with very depressed centra. As in this form, there is a facet on the transverse process of the first sacral for a corresponding one on that of the last lumbar. None of the caudal vertebræ are preserved.

The *limbs* of *Hyracodon* show even more striking divergences from the Rhinoceros type than does the trunk. One is immediately impressed with their lightness and length. The humerus is much like the corresponding bone in the Tapir and *Hyrachyus*, but of lighter construction; the head is very flat, about the same shape as in the Rhinoceros; the tuberosities are large and enclose a deep bicipital groove betwen them; but neither they nor the deltoid ridge are developed to anything like the extent that is seen in the Rhinoceroses. The shaft is slender, the trochlea rather narrow, and the condyles insignificant. The proximal end of the radius covers the entire width and most of the thickness of the trochlea, the ulna bearing very little of the weight. The shaft of the radius is slender, compressed and curved; its lower end is expanded for the reception of the scaphoid and lunar; but these faces are very small and narrow as compared with the same in *Hyrachyus*. The shaft of the ulna is very slight and is closely applied to the radius, though not co-ossified with it; its distal end is very narrow and articulates with the cuneiform only.

The *manus* as a whole is strikingly long and narrow, the carpus being especially contracted in width. Compared with the carpus of *Hyrachyus* the bones of the proximal row are all much narrower and vertically elongated. In the distal row the magnum is proportionately a much larger bone, following the relative increase of the middle digit, while the unciform has become very much smaller owing to the loss of the fifth digit, and the great reduction in size of the fourth. In like manner the trapezoid is much narrower, owing to the reduction of the second metacarpal. A trapezium was also present, but does not seem to have reached the scaphoid. As Prof. Marsh has shown, all the feet are tridactyle. The metacarpals are very elongate, and the third one is proportionately better developed than in *Hyrachyus*, but has very much the same shape as in that genus; the second and fourth metacarpals are very slender; they lie somewhat behind the third and are closely applied to it throughout their entire length, giving a very narrow and compact foot. The second metacarpal touches the magnum by a very small facet indeed, and differs in this respect very markedly from *Hyrachyus*, the Tapir, *Aceratherium* and the Rhinoceros. This state of things is also seen in the carpus of *Anchitherium*, and indeed the manus as a whole is not very unlike that of the American species of *Anchitherium*, in which the lateral metacarpals are less reduced in size than in the European species. The phalanges of *Hyracodon* are long and narrow, the ungual phalanges being especially so. They are not at all like the broad, flat unguals of *Hyrachyus*, but are narrow and pointed, somewhat like those of an antelope in general shape. The median unguals are missing from our specimens; probably they were broader than the lateral ones.

In the *hind limb* we find a similar series of modifications. As far as can be judged from our specimens, the pelvis was much like that of *Hyrachyus*, with the ilia less expanded than in the Tapir or Rhinoceros. The former is very much like that of *Hyrachyus*, but a little stouter; it is a long, slender bone, much lighter in construction than that of the Tapir or Rhinoceros; the head is set on a more decided neck and is more nearly spherical than in these forms. All three trochanters are well shown, but they have not the massiveness of these processes in Rhinoceroses. The construction of the trochlea and condyles is like that in *Hyrachyus*. The tibia is quite like that of the last-named genus, but a little stouter, though much more slender than in the Rhinoceros, Tapir or *Aceratherium*. The spine and cnemial crest are much less marked than in the three last-named genera, but heavier than in *Hyrachyus*.

The *pes* is narrow and compact like the manus. The astragalus is very like that of *Hyrachyus*, but narrower and with a shorter neck. The cuboid facet is very small, a striking contrast to the Rhinoceros type of astragalus, and a resemblance to the Lophiodont and *Anchitherium* types. The calcaneum is a little stouter and heavier than in *Hyrachyus*. The cuneiforms were all free. The metatarsals are very similar to the metacarpals, the median one being flat and straight, as well as slender and elongate; the two lateral ones are much reduced in thickness, and lie somewhat posterior to the plane of the median.

It will be evident from the foregoing description that *Hyracodon* was a very different animal from any other member of the Rhinoceros series, being a lightly built, slender, running animal. In short, it was a cursorial Rhinoceros, and all its modifications went towards adapting it to swift locomotion, as is seen in the long neck, the delicate limbs and the elongated, narrow feet. The reduction of the lateral metapodials indicates that the animal was not an inhabitant of marshes and jungles, and, as it was entirely devoid of weapons of defence, its only means of escape from its enemies lay in flight. One can hardly help believing that, had this line persisted, it would have resulted in a unidigital type, just as the tridactyle *Anchitherium* of the Miocene has terminated in the Horse.

As yet we do not know of any forms intermediate between *Hyracodon* and *Hyrachyus*. Possibly such a form may be found in the genus *Triplopus* (Cope). This animal resembled *Hyrachyus* in its dentition and skeleton, except that it had only three digits in the manus. But we have seen reason to believe that there was a common ancestral form for the three Rhinoceros lines, which had four digits in the manus and molar teeth of the Rhinoceros pattern. This reduction of the fifth digit can of itself hardly be regarded as any sign of direct relationship, as we find it taking place independently in so many different groups. We do not, therefore, regard it as probable that *Triplopus* stood in any direct genetic relation to *Hyracodon*.

THE DICERATHERIUM SERIES.

The third line of the Rhinoceros series consists of the very peculiar and interesting genera, *Colonoceras* and *Diceratherium*, of Prof. Marsh. The former differs from *Hyrachyus* only in the possession of a pair of rudimentary horn-cores placed transversely on the nasal bones; the latter is a large Rhinoceros with a pair of transversely placed nasal horns. It is very difficult to believe that this line, comprising the only horned Rhinoceros yet found in America, arose and acquired all the Rhinoceros characters of dentition and skeleton entirely independently of the line which passed through *Amynodon* and *Aceratherium*. It is possible that *Orthocynodon* may belong in this two-horned series rather than in the other; a supposition which finds support in the character of the molar teeth, which are closely alike in the two genera. But until the nasal bones of the Eocene genus are found this point must be left in doubt. Two other suppositions are possible with regard to this question:

(1) That *Colonoceras* is the ancestor of all the Rhinoceros lines, the nasal horns persisting only in the *Diceratherium* series and becoming atrophied in the others.

(2) That the transversely placed nasal horns arose independently in *Diceratherium* and *Colonoceras*. Of these two explanations the former seems the more probable, yet we cannot decide between them until further material is obtained. But if we are shut up to the alternative between the second explanation and the entirely independent origin of the hornless and transversely horned series, it must be admitted that it is far more probable that horns arose independently in *Colonoceras* and *Diceratherium* than that the latter should have acquired the characteristics of the Rhinoceros skull, skeleton and dentition, without any connection with the other series to which its structure closely allies it. At all events, the *Diceratherium* line seems to have diverged from the main stock before the appearance of the hornless *Amynodon*.

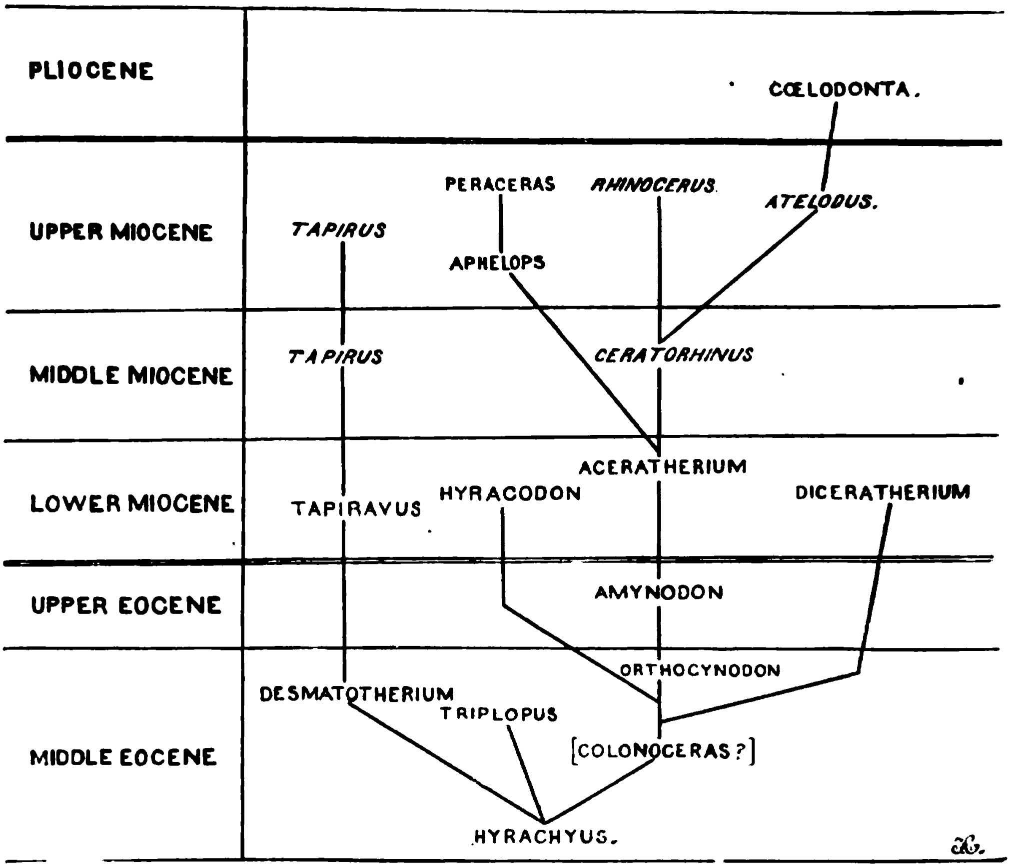
It is to be hoped that future discoveries will clear up these obscure problems, a solution of which the materials at present known will not enable us to offer.

The table on the following page will perhaps serve to make our views on the inter-relations of these various groups somewhat more intelligible. In several respects it will be found to agree with that already published by Prof. Cope.

In conclusion a few words as to the generic names that have been repeatedly used in this paper. Subsequent discoveries have made it necessary to revise Prof. Cope's excellent table[1] of the genera of this group, some of which must be suppressed and some new ones are to be added.

Mr. Lydekker[2] has shown that the genus *Zalabis* (Cope) was established on a misunderstanding and must be dropped, but we cannot agree with this author in uniting *Aceratherium* and *Aphelops*. The fact that the number of toes cannot always be ascertained is certainly no reason for this union; any such system would at once throw scientific nomenclature into the direst confusion. Mr. Lydekker also concludes from *plaster casts* that the auditory meatus is closed below in *Aceratherium*. The figures

[1] Amer. Nat., 1879, p. 771.
[2] Palæontologia Indica, ser. x. vol. ii.



(*Names in italics are those of genera still living.*)

of Gaudry, Pictet and De Blainville show the meatus open, as is certainly the case in all the American species.

We also think it better to preserve the generic names that have been given to the three living types of Rhinoceroses, as it seems to us that their differences entitle them to such separation.

The writers wish to express their indebtedness to Curator Franklin C. Hill, for his valuable assistance in the preparing and mounting of the fossils described in this and the following papers.