RIBUTIONS FROM THE E. M. MUSEUM OF GEOLOGY AND ARCHÆOLOGY OF PRINCETON COLLEGE.

BULLETIN No. 3.

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

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BY

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PRINCETON, N. J., MAY, 1883.

I.

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

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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

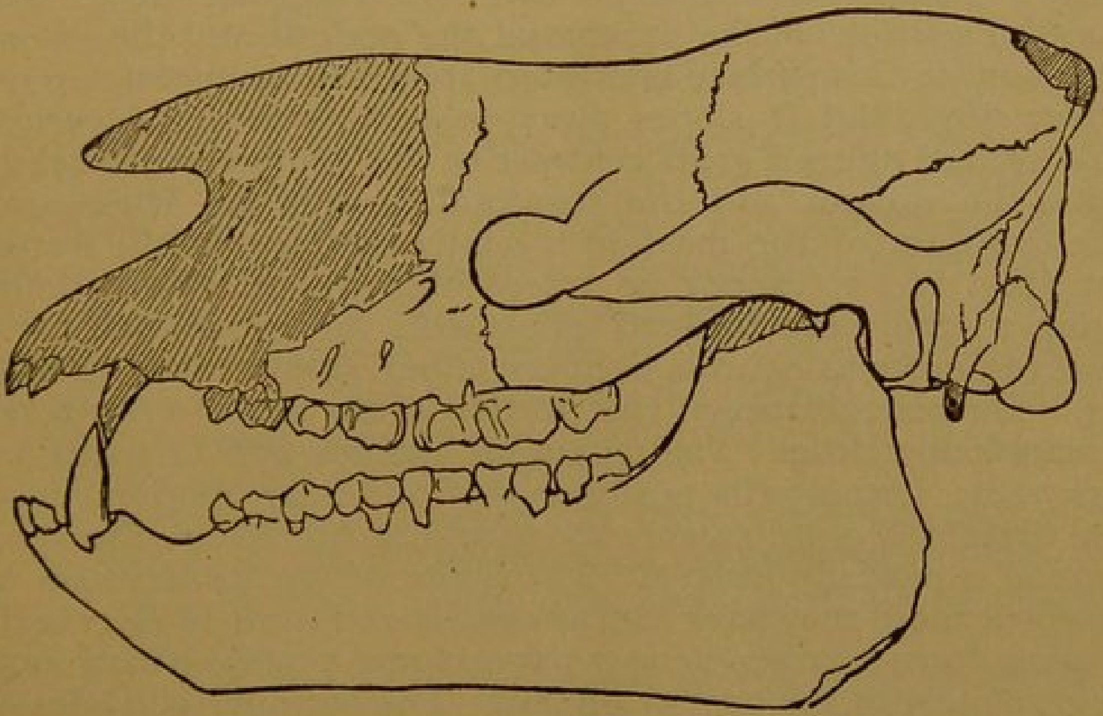

Fig. 1.—Restoration of Orthocynodon. (One fifth natural size.)

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.

fossa of the first molar, and the greater size of the posterior lobe of this tooth, as compared with the more modern types.

UPPER JAW. *Incisors.* One isolated tooth is preserved which probably belongs to this series. It is more distinctly acute and conical than the corresponding lower incisor. As in the latter there is an internal cingulum and a ridge running down the inner face of the crown. The edge is considerably worn.

The *Canine* is not preserved, but its presence is demonstrated by the worn posterior surface of the lower canine. The size and shape of this worn surface would seem to indicate that the upper canine was smaller than the lower, though little dependence can be placed on this.

Premolars. Of this series only the third and fourth are preserved, and the inner part of the crown of the third is badly broken. The external face of this tooth shows that the antero-external lobe is not so much reduced as in the true molars. This face is sub-quadrate in outline, but with the cutting edge shorter than the base. The ridge separating the two lobes is distinct. There seem to have been two transverse crests which may have been distinct or united in one internal lobe, but the inner part of the crown is so broken as to render either view uncertain.

The structure of the fourth premolar differentiates this genus from *Amynodon* in being constructed on essentially the same plan as the molar teeth, though with some modifications. The antero-external lobe is not so much reduced as in the molars, and there is a distinct ridge on the outer face of the hinder lobe. There are two transverse crests which are independent internally; the posterior one is, however, very low. A strong cingulum runs around the whole interior of the crown.

The *Molars* are of the typical Rhinoceros type, though simpler than in the recent or even the Miocene forms. Mr. Lydekker[1] has shown that the upper molars of the *Rhinocerídæ* may be divided into two classes; one of these, represented among recent forms by the Sumatran Rhinoceros, "is characterized by the production of the antero-external angle of the crown into a strong buttress or column, which renders the outer wall of the tooth very sinuous. . . . . The second type of molar is represented in the large living Indian rhinoceros and in the African rhinoceroses; it is characterized by the absence of the buttress, whence the external wall is approximately straight." The first of these types is the older one, and to it *Hyracodon* and *Aceratherium* (at least so far as the American species are concerned) conform. This is also true of *Orthocynodon*, which has the molars less complicated even than in *Aceratherium*. Prof. Cope[2] has called

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[1] Mem. Geol. Survey of India, Palæontol. Ind., ser. x., vol. ii. p. 8.
[2] Bulletin U. S. Geolog. Survey, vol. v. no. 2, p. 231.

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

[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-

[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

[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.

It seems to us, therefore, more likely that the Old World forms were derived from *Aceratherium* through *Ceratorhinus*, while *Aphelops* and *Peraceras* were the American forms derived likewise from *Aceratherium*. This view does not preclude the possibility of a migration of *Aphelops* from America, and it would not be surprising if such were found to be the case. Perhaps the genus is still living, and may be represented by the *R. inermis* of Lesson.[1] The view here maintained is simply that *Aphelops* cannot be regarded as ancestral to any of the modern genera.

This conclusion is confirmed by a comparison of the molar teeth of the species from America with those of the Old World forms. In the American *Aceratheria* the only complication of these teeth consists in the bulge projecting from the *anterior* transverse crest into the median valley. This is also found in some of the European forms, though the latter, as well as those of India, agree with the modern species in having these accessories developed on the *posterior* transverse crests. *Aphelops* has something of both, while the modern species (at least as many as we have had the opportunity of examining) agree with most of the Old World species of *Aceratherium* in having the anterior crests of the molars simple.

THE HYRACODON SERIES.

This most interesting offshoot of the Rhinoceros line has long been imperfectly known. Professors Leidy, Cope and Marsh have given us valuable hints with regard to its structure, but there still remains much to be done in this respect.

Among the collections made by the Princeton Expedition of 1882 was a large number of *Hyracodon* specimens, including an almost complete skeleton. This material serves to throw much light upon the structure of this animal and its place in the zoological system.

Hyracodon was a slender, long-limbed and slightly built animal with a long neck and delicate head. Its proportions were those of a Horse rather than of a Rhinoceros. It is evidently very closely related to *Hyrachyus* (as was suggested by Prof. Marsh from the character of the molar teeth), and many parts of its skeleton were almost identical with those of the latter genus.

In its general features the *skull* is of the Rhinoceros type, but, as we have already seen, there are many points of resemblance to the *Hyrachyus* skull; the long sagittal crest, the weak nasal bones, the widely open auditory meatus, the shape of the

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[1] See Cope, Bull. U. S. Geolog. Survey, vol. v. no. 2, p. 237.

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 cne-

mial 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

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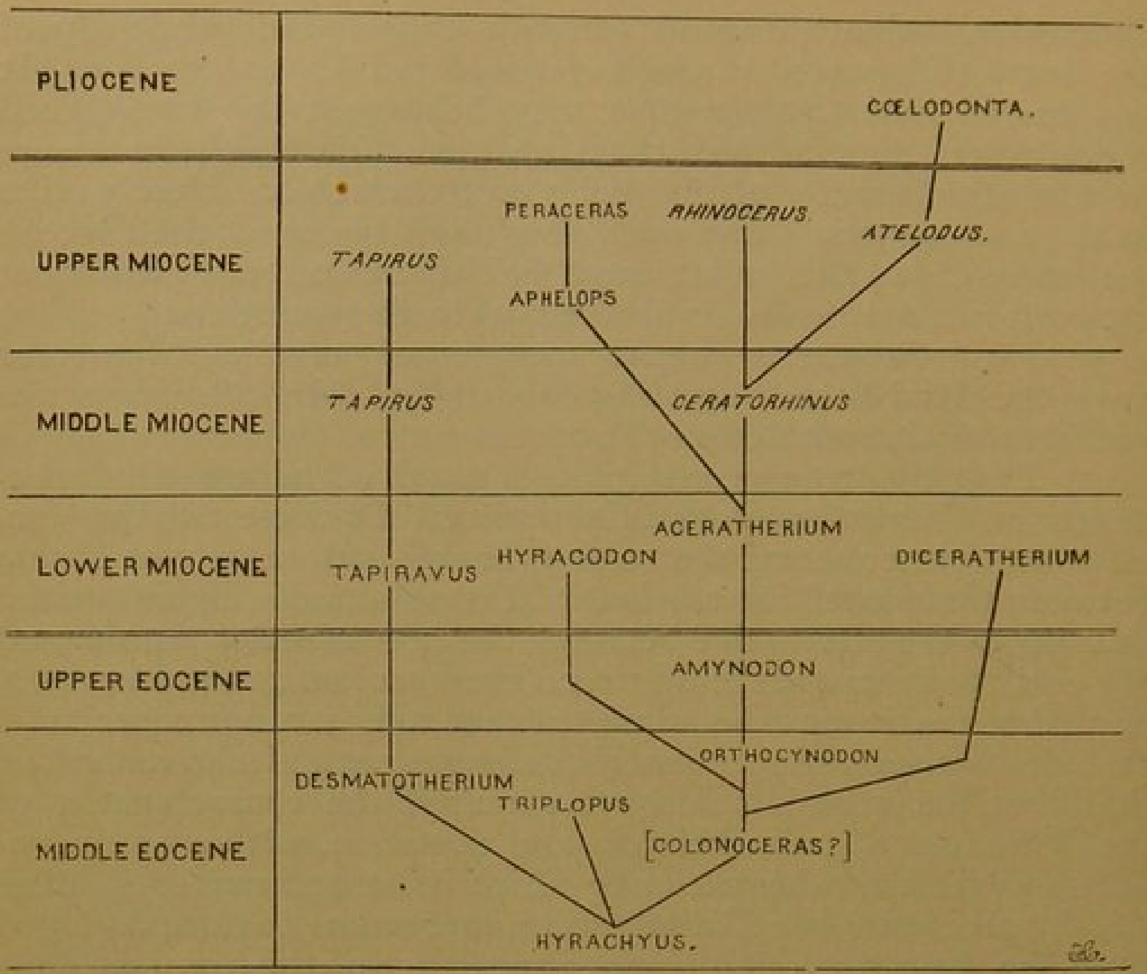
[1] Amer. Nat., 1879, p. 771.

[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.

II.

ACHÆNODON, AN EOCENE BUNODONT.

HENRY F. OSBORN.

Achænodon is probably the oldest of the Pig family which has as yet been discovered. It is thus far known only by the skull and lower jaw. The structure of these parts relates the animal with *Entelodon* and *Tetraconodon*[1] among the *Suina Bunodonta.* The general appearance and character of the skull are, however, much less like those of an Ungulate than like those of a large Carnivore.

History of the Genus. The mandible of *Achænodon* was discovered by Professor Cope in 1872;[2] he distinguished it from *Entelodon*,[3] which Leidy had previously found in the Dakota Miocene, by the fact that it had a strong posterior lobe on the last lower molar. He left the number of premolars uncertain. Professor Marsh in 1876 found the complete lower jaw of a similar animal, which he referred to a new genus, *Parahyus*.[4] He noticed the likeness to *Entelodon*, distinguishing the genus by the fifth lobe of the posterior lower molar, also by the fact that there were but three premolars. The mandible of the skull in the Princeton collection agrees with each of these descriptions, although the number of premolars is somewhat doubtful.

With our present knowledge the genus *Achænodon* cannot be clearly distinguished from *Tetraconodon* except by the presence of a few minor tubercles upon the slopes of the molar cusps in the latter genus. The resemblance between the premolars, with their high conical crowns, is striking, and both genera agree in possessing the fifth lobe on the last lower molar.

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[1] Memoirs of the Geological Survey of India: Palæontology, ser. x. vol. i.—Lydekker.

[2] U. S. Geol. Surv. of the Territories, 1873, p. 456.

[3] In regard to the use of the generic name *Entelodon* in preference to *Elotherium*, see Kowalewsky, Palæontographica, xxii. p. 415. Leidy has employed the latter name; Kowalewsky shows that the former has the precedence.

[4] Am. Journ. Science and Arts, 3d series, vol. xii. p. 402.

The specimen in the Princeton collection consists of the greater portion of the skull and the right mandibular ramus. It was obtained by the Expedition of 1878 at the bottom of the Bridger Beds (Middle Eocene) of Wyoming, and was thus coeval with *Uintatherium*, *Hyrachyus*, *Palæosyops*, *Orthocynodon*, and other Ungulates of this period:

Generic Characters.

Dental formula: $i. \frac{3}{3}, c. \frac{1}{1}, pm. \frac{3}{3} \text{ or } \frac{4}{4}, m. \frac{3}{3}.$

The last lower molar has a fifth fang and posterior lobe; the other molars are of the Bunodont type with four simple cusps; the premolars have high conical crowns; the incisors vary in size—in some adults the lateral incisors may be wanting; the glenoid fossa is deep and has a wide anterior border.

Several of these characters distinguish *Achænodon* from *Entelodon*. The species[1] of this genus may be doubtfully stated as follows: *Achænodon insolens*, Cope. Lower incisors three in number, subequal in size; probably four lower premolars, the anterior being rudimentary.

Achænodon (*Parahyus*) *vagus*,[2] Marsh. A small species. Lower incisors subequal in size; three lower premolars.

Achænodon robustus, Osborn. A large species. Median and lateral incisors rudimentary or wanting; premolars three or four; accessory tubercle upon postero-internal cusp of last superior molar.

ACHÆNODON ROBUSTUS.

DESCRIPTION OF THE SKULL.

The *Skull* (Plate VI) is about eighteen inches long and, including the lower jaw, about ten inches deep. It is thus broad and deep in proportion to its length; the facial and cranial regions are in about equal proportions and arch upwards posteriorly. The brain-case is small, but the zygomatic arches are broad and strong, and the occiput is rather high and narrow in proportion.

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[1] Professors Marsh and Cope have both kindly allowed an examination of their specimens.

[2] Prof. Cope is inclined to consider *Parahyus* as a genus distinct from *Achænodon*, from the fact that it has but three premolars; but from the uncertainty as to the number of premolars in *Achænodon*, and the close agreement of the lower teeth in other particulars, it seems better to retain the single generic name at present.

The zygoma arches widely outwards from the side of the ear region, then turns abruptly forwards, ascending slightly towards the orbit. The orbit is small, placed midway between the anterior end of the canine and the post-glenoid process. It is directed slightly forwards and upwards. It is uncertain whether the orbit was completely surrounded by bone. The post-orbital processes of the malar and frontal are strong, and indicate that the post-orbital ring was complete. There are slight supra-orbital rugosities.

On the upper surface of the skull the supra-orbital ridges converging form a short wide V. They unite in a sagittal crest which arches upwards and backwards; it recalls the *Palæosyops* crest, except that it forms a comparatively thin edge. Important characters are found at the back of the skull, which unfortunately is somewhat distorted. The occiput rises obliquely backwards; it is broad and quite deeply concave, suggesting the Pig, although somewhat lower and broader. The *basi-occipital* bones and occipital condyles are wanting as well as the *basi-* and *pre-sphenoids*. One of the most exceptional features of the skull is the shape of the glenoid cavity (see Fig. 7 : 2); it is about three inches broad, with well-raised anterior and posterior margins; it is therefore, like that of the Bear, quite deeply concave in fore and aft section, and plane in transverse. The post- and pre-glenoid margins are broad, not narrow, and tubercular as in the Peccary. Returning to the facial region, we find that the limits of the *lachrymals* extend some distance upon the face; an important character. The union of the *malar* and *squamosal* is well defined; the latter is nearly flat on its lower surface, with a rugose border for the mandibular muscles, and curving downwards posteriorly; anteriorly the malar extends about half way up beneath the orbit, forming a small portion of the face.

The *maxillaries* are short, rounding inwards and perforated by the infra-orbital foramen immediately behind the canine. The *nasals* are much broken and distorted in our specimen; the forward portion is wanting.

The *lower jaw* is in fine preservation. The ramus is long in proportion to its depth, arching slightly downwards and thickening beneath the molars. There is a slight tuberosity beneath the first premolar; above this is the mental foramen. The condyle is over two inches broad and well raised above the level of the molars. The upper margin of the jaw sinks and then rises an inch and a half, forming the coronoid process; from the forward portion of the coronoid a strong flange passes down the external face of the ramus. The angle has a gently rounded and rugose border, with a deep fossa for the masseter muscle, and is completely overhung by the condyle. The symphysis is oblique and long, extending back to a point beneath the second premolar.

Measurements.

Skull.	M.
Distance from post-glenoid process to anterior end of canine	.31
Anterior edge of orbit to anterior end of canine	.15
Diameter of orbit	.04
Distance between zygoma and side of skull (3½ inches)	.087
Width of glenoid cavity, transverse	.08
Depth between glenoid ridges	.015
Estimated height of skull above last molar (5¼ inches)	.15
Approximate length of skull (about 18 inches)	.46
Mandible.	
Depth of ramus below posterior molar	.089
Distance from angle to anterior end of symphysis (about 14 inches)	.37
Height of coronoid above the mandibular condyle	.06
Transverse diameter of the condyle (fractured)	.06
Elevation of condyle above level of angle	.125

DENTITION.—The teeth are quite well worn in some places, indicating an adult growth. The upper incisors are wanting, but were probably of the same number as the lower. In the latter series the second incisor is large. The incisor alveolus is short; if the first and third incisors were present they were rudimentary. The number of premolars in each jaw is also uncertain; the formula cannot, therefore, be stated positively. The teeth present characters which indicate an omnivorous diet, with strong carnivorous crowns in the anterior portion of the jaw. The *upper molar* series is six inches long, arching outwards from before backwards and diverging rapidly. The crowns of the upper molars (see Plate VI, Fig. 2) are nearly quadrate in shape, with smooth convex inner sides and a slight basal cingulum on the outer side. They each have four not very strongly marked lobes, sub-equal in size, except the last molar, in which the posterior lobes are much compressed. Each lobe rises to a low conical cusp, and these cusps are placed in transverse pairs. On the postero-internal lobe of the last molar is a small accessory tubercle, and there are very slight traces of these median tubercles on the other molars, suggesting the teeth of *Entelodon*, in which animal each molar bears six cusps placed in transverse rows of three each.[1] Although it does not appear so from the measurements given, the second molar is the largest owing to the larger size of the posterior lobes. The molars have two outer fangs and one inner double fang. Many of the molar cusps show a slight tendency to become crescentoid, a feature which is quite marked in *Achænodon vagus*.

The *upper premolars* have high pointed crowns with a slight basal cingulum.

The low anterior and posterior ridges bounding the inner angles of the teeth present a feature important in the consideration of the carnivorous resemblances of these teeth. The first and second premolars are two-fanged, the latter tooth set somewhat obliquely to the jaw. The third premolar has a high crown

[1] Leidy, Ancient Fauna Nebraska, vol. vi. Smithson. Contributions to Knowledge, Plates VIII–X.

with a strong, low inner cusp; it is three-fanged. The *canines* are large, recurved and slightly oval in section; they recall those of *Hyænodon* or *Ursus*. If the tips were unworn they would extend fully an inch and a half below the line of the premolars.

The *lower incisors*, judging by the sockets, are very compactly placed, almost in a semicircle between the canines, and directed obliquely upwards and forwards. Their position differs from that in *Entelodon*, where the alveolus is long and the teeth are placed widely apart. We possess the second incisor on each side below; the indications are that the medial and lateral incisors, if present, were extremely small. Two incisors which we suppose belong to the upper jaw are much smaller than the lower second incisors. All these teeth are worn very blunt; there is evidence, however, of an anterior cutting edge and a low cingulum behind. In Professor Cope's specimen the incisor alveoli are perfect, although the teeth are wanting; the teeth were arranged almost in a semicircle, appearing to have diminished in size towards the centre.

The *lower molars* resemble the upper, but are more compressed laterally. The first is the smallest molar in each jaw. Another feature is that the inner cusps are smaller than the outer. A generic character is found in the last lower molar, which possesses a strong posterior lobe and fang, as in the Pig. Judging from the Princeton specimen only, it would be difficult to determine positively the number of premolars. Cope in his brief description of *Achænodon* left it uncertain. Marsh described them positively as three in number in *Parahyus*. Behind the canine in our specimen is a small followed by a large socket; the former may have held a rudimentary single-fanged *premolar*, while possibly the two sockets held one double-fanged tooth. A peculiarity of these teeth is that they are placed close together, although not quite in contact. The last lower premolar is the largest of the series, but does not resemble the corresponding upper tooth in possessing an internal lobe.

Measurements of Teeth.

Lower Teeth, as worn.

	Vertical diameter of crown. M.	Antero-posterior diameter of crown. M.	Transverse diam. of crown. M.
canine,	.065	.030	.026
2d premolar,	.016	.024	.015
3d premolar,	.019	.029	.017
1st molar,	.01	.024	.017
2d molar,	.011	.026	.02
3d molar,	.012	.035	.022

Upper Teeth.

	Vertical diameter of crown. M.	Antero-posterior diameter of crown. M.	Transverse diam. of crown. M.
canine,	.066	.032	.028
2d premolar, (oblique,)	.02	.028	.018
3d premolar,	.02	.022	.028
1st molar	.006	.021	.026
2d molar	.01	.024	.031
3d molar	.015	.028	.029
incisor	.011	.013	.012

Total length of upper molar series (about 6 inches) .... .15 m.
Total length of lower molar series (about 7 inches) .... .175 m.

Ordinal Position of Achænodon. In general characters *Achænodon* presents a closer resemblance to *Entelodon* than to any

other form. *Entelodon* (Pomel), first found in the Tertiary of Europe, was discovered by Leidy in the American Miocene. He at first referred it to *Archæotherium*,[1] but later ascertained its true position.[2] This resemblance establishes *Achænodon* as an Ungulate, but it differs widely from the modern Ungulate type in the conformation of its skull. It has some resemblances to the Bears, and some marked suilline features.[3] There follow a series of comparisons with several animals with which it has points of structure in common.

Likeness to Entelodon. The discovery of the skull adds to the number of characters distinguishing *Achænodon* from *Entelodon*, besides those which have been already noticed in the lower jaw. The generic distinctions of *Achænodon* may now be stated: (1) the probable loss of the anterior premolar in each jaw; (2) four cusps on the superior molars; (3) a fifth or posterior lobe on the

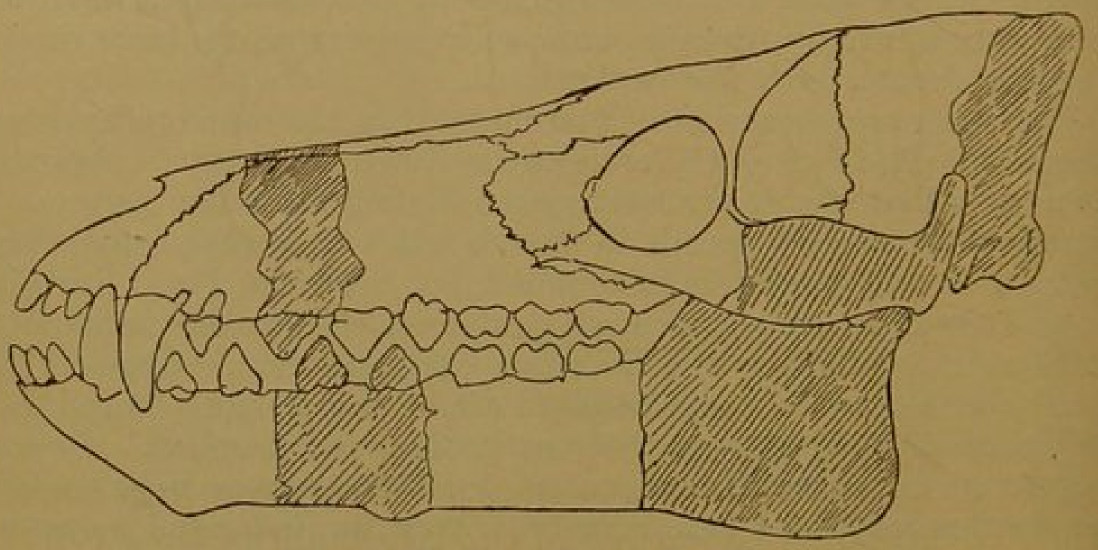

Fig. 2.—Skull of a Young Entelodon.

last lower molar. Some species of *Entelodon* possess but four cusps on the superior molars, according to Kowalewsky. In most respects *Achænodon* has less of the suilline type than *Entelodon;* the fifth lobe of the last lower molar is an exception to this fact. The canines of some of our *Entelodon* specimens are flattened behind as in the Pig; those of *Achænodon* are rounded. The molars of the former genus resemble those of *Chæropotamus*, while the molars of *Achænodon* resemble those of the oldest *Suidæ*, such as *Palæochœrus*. The teeth of *Achænodon* are also set in a more compact series. In lateral view the skull of *Achænodon* is shorter and deeper; the face is less elongated than that of *Entelodon;* the post-orbital region is

[1] Ancient Fauna Nebraska, loc. cit.

[2] Extinct Fauna of Dakota and Nebraska, Plate XVI, p. 175.

[3] The points of structure connecting *Achænodon* with *Tetraconodon* have been enumerated above; the molars of the latter, with the accessory tubercles, show a nearer approach to the modern Pig or Hippopotamus type.

less elevated. A more important difference is seen in the peculiar shape of the glenoid fossa. On the other hand, an unmistakable affinity between the two genera is indicated by the general likeness in the dentition. Minor resemblances are seen in the mammilary tuberosities on the lower jaw, the shape of

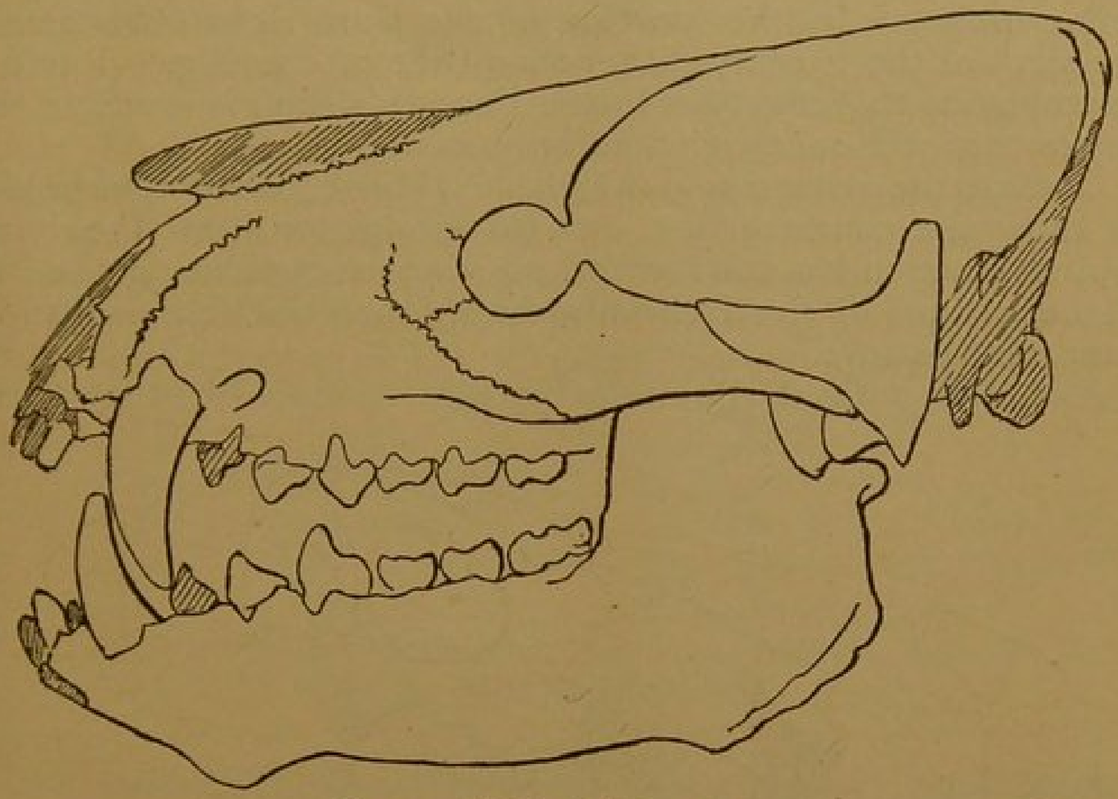

Fig. 3.—Skull of Achænodon.

the angle of the jaw, the small size of the first lower molar. The drawings are restorations of the two skulls in the Princeton Museum, the *Achænodon* skull, also the skull of a young individual of *Entelodon*, assisted by Leidy's restoration.

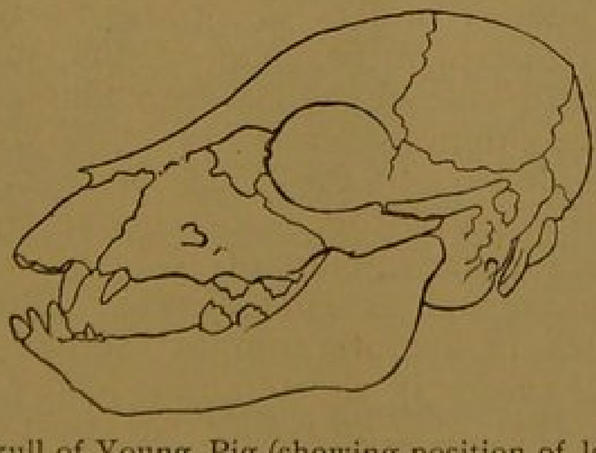

Fig. 4.—Skull of Young Pig (showing position of lachrymals).

Comparison with the Suidæ. The Pig characters are mostly contained below a line drawn forwards from the external auditory meatus within the zygoma, then downwards behind the

last lower premolar; in other words, these characters predominate in the upper and lower molar series and the back part of the mandible. Here are marked suilline features: (1) the four-cusped molars of the Bunodont type; (2) the rounded angle of the jaw; (3) the erect coronoid; (4) the somewhat elevated mandibular condyle; and (5) the fifth lobe on the posterior molar. In this portion of the skull *Achænodon* recalls the skull of the Peccary rather than that of the Pig. Further resemblance to *Achænodon* in the Peccary's skull is found in the narrow but well-raised glenoid borders.

Outside the general region indicated above, the occiput begins to show the characteristic upward elongation, and the infra-orbital foramen has the forward position which it has in the Pig. The exposure of the lachrymal bone upon the face is also an important feature.

As before noticed, the molar pattern is more like that of the

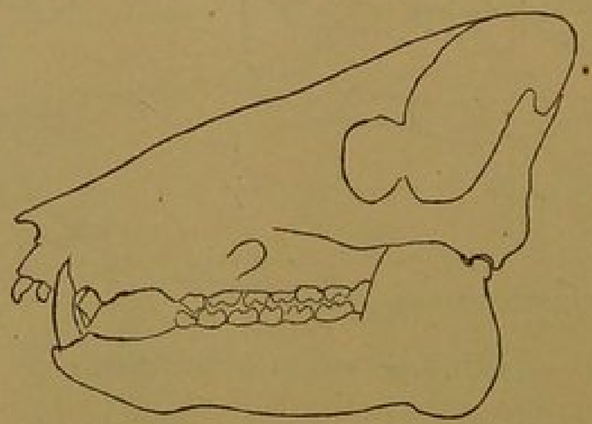

Fig. 5.—Skull of Peccary.

oldest of the Pig family than that of any of the modern forms; this arises from the simplicity of the molar cusps, which entirely lack the lesser tubercles found in *Sus scrofa*, for example, and are more like the cusps of *Sus antiquus*.[1]

While the above characters, which have a generic importance, relate *Achænodon* to the Ungulates, the structure of the skull is remarkable for its likeness to that of some of the *modern and ancient Carnivores*. This conformity of structure was at first regarded as indicating relationship, but this view was soon abandoned. The following homologies are pointed out as bringing out one of the most interesting phases in early Ungulate history—that of the adaptation of the skull partly to self-defence, partly to a mixed diet. Except for the elevated occiput, the actual size and proportion of the posterior and upper portions of the skull are almost identical with those of the California Bear (*Ursus arctos*). This likeness extends to the sagittal crest,

[1] DeBlainville, Ostéographie, vol. iv.; G. Sus, pl. viii.

to the shape and relative position of the orbit, as well as the bones of the zygomatic arch, the mandibular condyle and glenoid fossa. The last feature is, so far as we know, unique among the Ungulates. A comparison of Fig. 7: 1 and 2 shows the ursine shape of the glenoid fossa, also that in the development of a broad, well-rounded pre-glenoid border it differs from the *Palæosyops* (Fig. 7: 3) type, which closely resembles that

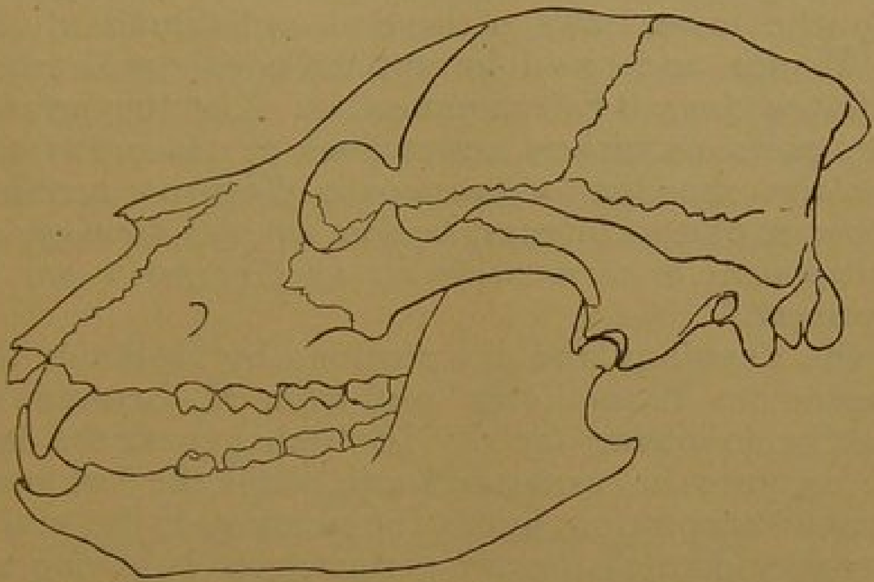

Fig. 6.—Skull of Ursus arctos.

of the modern Tapir. The angle of the jaw is much deeper than in any of the Carnivores, and the condyle is slightly more elevated. The premolars resemble those of *Hyænodon* in side view, but they are more obtuse and have not been worn by lateral attrition as in the Carnivora. The canines are blunted at

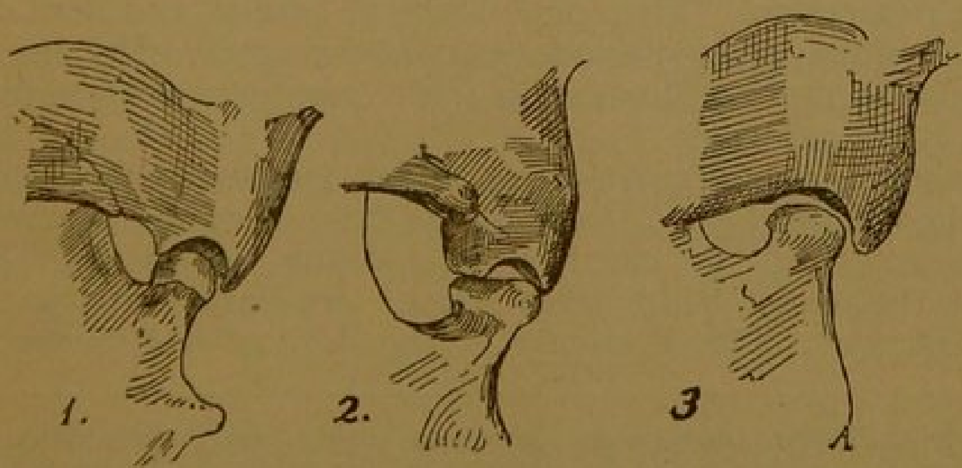

Fig. 7.—Glenoid fossæ: (1) of the Bear; (2) of Achænodon; (3) of Palæosyops.

the tips as in some old bears. The last upper premolar with its inner fang and heel suggests the carnassial tooth, but it is not opposed by any tooth corresponding to the lower carnassial.

The above resemblances are mostly to characters found in the

oldest group of Carnivora, the *Arctoidea*,[1] which includes the Bears, Raccoons, Weasels and allied forms. Among extinct forms there is a strong likeness to some of the *Creodonta*, especially to the genus *Arctocyon*[2] of DeBlainville.

Our knowledge of *Arctocyon* is sufficient for comparative purposes and it is interesting to note that *Achænodon* and *Arctocyon* each have the same likeness to the Pig and the Bear. The following paragraph by M. Lemoine[3] is significant; it relates to the lower jaws of several individuals of *Arctocyon* found in France, and could be applied with equal truth to the jaw of *Achænodon:* " Effectivement si l'Arctocyon tient des carnassiers par ses incisives, ses canines et ses prémolaires; ses arrière-molairs rapellent à beaucoups d'égards certains types des Porcins, et chose curieuse, *la dent la plus développée chez les autres carnassiers, la carnassière est ici plus petite que les dents qui l'avoisinent.*"

From the drawings and descriptions by DeBlainville in the Ostéographie des Mammifères[4] and from M. Lemoine's articles we derive the following facts.[5] In both genera the last upper premolar suggests the carnassial tooth, while the first lower molar has no similar adaptation, but is the smallest of the molar series. The lower premolars of the two genera agree in having two roots and high, single, compressed crowns. In *Arctocyon Gervaisii*, as in *Achænodon vagus*, there are but three lower premolars, but the last inferior molar lacks a posterior heel. The upper molars of each animal are suilline. They resemble each other further in the ursine shape of the condyle and glenoid fossa. There is a great disparity in size between the two genera, *Arctocyon* being much the smaller. Accurate comparison with *Arctocyon* is difficult owing to the imperfection of the plates and descriptions in our possession. The coincidence of cranial and dental characters between *Arctocyon* and *Achænodon* is noteworthy, insomuch as it affords another illustration of the carnivorous specialization of the latter genus.

All the Eocene *Perissodactyla*, which are more or less allied to the Palæotherioid forms (see Fig. 8), have long been known to be characterized by carnivorous-looking skulls. *Orthocynodon* of the early Rhinoceros group presents somewhat similar characters. The discovery of the skull of *Achænodon* shows

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[1] See Prof. Flower, Class. of the Carnivora, Proc. Zool. Society, 1869.

[2] Professor Cope first called the attention of the writer to the resemblance of this animal to *Arctocyon*, and later to some of its apparently Creodont characters.

[3] Lemoine, Comm. sur les Ossements Fossiles, Soc. d'Hist. Nat. de Reims, 8 mai, 1878, p. 6.

[4] Tome ii., gen. Subursus, pl. xiii.

[5] Since I wrote the above M. Lemoine has sent me a copy of his " Étude du genre Arctocyon," Ann. des Sc. Nat., 1878, in which he compares the *Arctocyon* and *Entelodon* molars, and in which is found a full account of the dentition of *Arctocyon*.

that this is true of the suilline types as well, and can therefore be safely called a characteristic of all the Eocene Ungulates.

Kowalewsky, in a valuable article upon *Entelodon*,[1] has pointed out this carnivorous conformation of the masticatory apparatus among the Tertiary Ungulates as having affected the adjoining portions of the skull. It undoubtedly is much more marked among the Eocene than among the Miocene Ungulates, all of which are more of the modern type. A comparison of one of these older skulls with more modern forms shows that there has been (1) a gradual elevation of the mandibular condyle and diminution of the coronoid; (2) the orbit has been apparently moving backwards owing to the forward elongation of the face; (3) the sagittal crest and deep temporal fossæ have disappeared; (4) the zygomatic arch has been gradually weakening; (5) in the

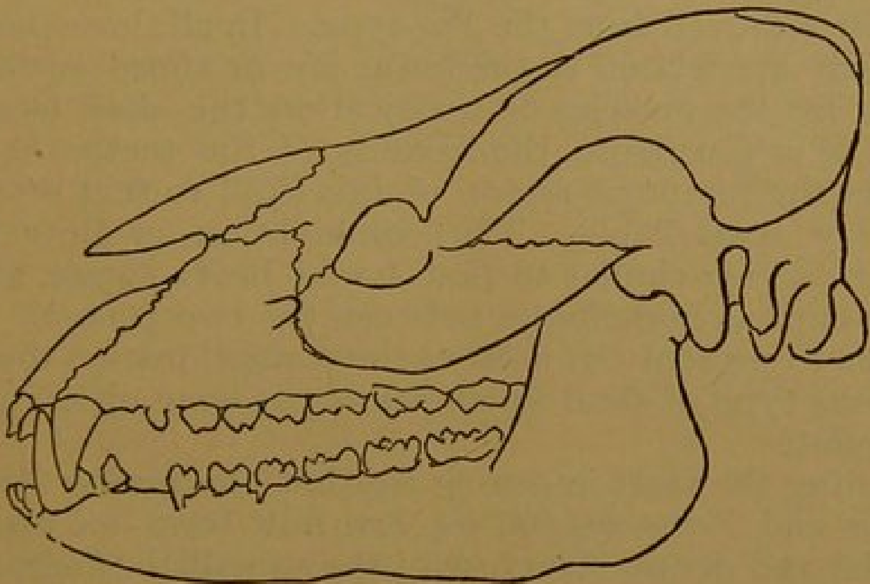

Fig. 8.—Skull of Palæosyops.

Ruminant line the post- and pre-glenoid processes have alike almost wholly disappeared; in the Perissodactyle line the pre-glenoid process has wholly disappeared, the post-glenoid has become a heavy downward process, undergoing a peculiar series of changes among the *Rhinoceridæ;* (6) the lachrymals have been extending upon the face.

CONCLUSIONS.

The study of *Achænodon* gives fresh contradiction to an old error that a certain type of structure which we are in the habit of considering as peculiarly characteristic of a single order of animals is necessarily confined to that order. Here among an ancient group of even-toed Ungulates is a carnivorous structure of skull which is so extreme that the real relationships of the

[1] Palæontographica, Band XXII, Seite 280.

animal were hardly at first detected. The peculiar conformation of different portions of the skull is apparently so far from that of an Ungulate that from the portions of the skull in our possession the likeness of the dentition to that of *Entelodon* was at first the sole ground for assigning it to the Ungulates; later the exposure of the lachrymal bone upon the face was discovered, and afforded independent evidence that the skull did not belong to any true Carnivore, although this would not exclude it from the Creodonts.

The characters of the teeth of *Achænodon* show that it is a near ally of *Entelodon*, although it possesses one less premolar and has an additional lobe on the last lower molar. This likeness places it among the ancestral *Suidæ*, although the characters of the feet are still undetermined. The elevation of the occiput suggests the modern Pig, but in most respects the skull is very far removed from the Pig type. In all those parts of the skull which are related to the lower jaw or afford surface of attachment for the muscles of mastication the skull is strikingly like that of a Carnivore, the likeness of the teeth, the glenoid fossa, and the temporal region of this skull to that of the Bear being very remarkable. The combination of Bear and Pig characters is very similar to that found in *Arctocyon*, and there are some curious homologies between the two genera. *Achænodon* seems to present the most extreme modification towards the carnivorous type of skull which has as yet been observed among the Ungulates.

By uniting the facts in our possession concerning *Achænodon*, *Entelodon* and *Tetraconodon*, we can now form an estimate of the cranial and dental structure of the ancesibal *Suidæ*, although the derivation of the group still remains obscure. The brain case of the early forms was small, surmounted by a high, thin sagittal crest which spread out in the upper occipital region, forming a very deep and extensive temporal fossa. The occiput was narrow and concave above, but lacked the extreme upward and backward elongation of the modern forms. The orbit, partially surrounded by bone, was small and placed midway between the occiput and incisor alveolus; the face, therefore, was short and rounded. In keeping with these proportions, the parietals were as long as the frontals (as in the young modern Pig, see Fig. 4),and the first indication of the elongation of the face was in the extension of the lachrymals and malars upon the face. The zygomatic arch was very powerful, standing out widely from the skull. The glenoid fossa was wide, with strong post, and pre-glenoid borders (the pre-glenoid border is strong in *Achænodon*, it is retained in a less degree in *Entelodon*, and probably is still represented in the pre-glenoid process of the Peccary's skull). The mandible was deep with a rounded angle and condyle, but slightly raised above the molars. There

were three molars in each jaw, which bore four simple conical cusps, the internal cusps being slightly smaller than the external; the third lower molar in some genera possessed a fifth posterior lobe. The premolars were four in number, with high, single, conical crowns, borne upon two fangs, except the fourth upper premolar, which had an internal lobe and third fang. The four canines were large, rounded, recurved and subequal in size. The incisors were three in each jaw, with anterior cutting edges, and almost erect in position.

III.

OBSERVATIONS UPON THE BRAIN CASTS OF TERTIARY MAMMALS.

By ADAM T. BRUCE.

Brain casts of fossil animals are intracranial moulds of the brain cavity, formed originally from a soft matrix which has subsequently solidified. The cranial bones may adhere to or become separated from the hardened cast. Casts from which the cranial bones have been separated are liable to fracture and weathering, which causes frequently render even approximate identification very difficult.

The casts which it is the purpose of this paper to describe, were, with the exception of a single Eocene form, collected from the White River Miocene of Colorado and Dakota. A detailed description of each cast will be followed by some general conclusions which their collective study seems to sanction.

The brain casts are figured in natural size in Plate VII.

UNGULATA.

ARTIODACTYLA (*Selenodontia*).

OREODON.

A series of brain casts, presenting the same general features, collected by the expeditions of 1882 and 1878 from the White River Miocene of Colorado and Dakota have been identified as casts of the cranial cavity of Oreodon. Proof has been mainly derived from the description of a brain cast of Oreodon given by Dr. Leidy, and from some Ungulate characters noticeable in the casts. The number of Oreodon remains found near the casts is additional evidence.

The gyri on the hemispheres make acute angles with the dorsimeson[1] posteriorly thus indicating an Ungulate type of

[1] Line marking dorsal boundary of mesal plane. See Wilder's "Anatomical Technology" for explanation of terms.

brain. Dorsally three prominent gyri are apparent on each hemisphere. Their configuration is quite similar in all cases. A fourth gyrus, the sylvian, is apparent laterally above the hippocampal lobe. These gyri, according to Owen's nomenclature, would be the median, medilateral, supersylvian and sylvian. The median, in all cases, runs forward to a point on the line drawn at right angles to the dorsimeson from the anterior extremity of the temporal lobe, where it becomes continuous with the medilateral in some cases; in others, it bifurcates, becoming continuous with the orbital as well as with the medilateral gyrus. In the specimens represented by Figs. 1 and 3, a well-defined groove formed by the confluent lateral and supersylvian fissures, extending mesad, partially separates the median from the orbital gyrus. In specimens represented by Figs. 2 and *2a*, the median gyrus appears to be continuous with the orbital. The supersylvian gyrus is well defined, terminating in all cases anterior to the medilateral. The sylvian gyrus is separated from the supersylvian by a well-defined fissure. Its anterior termination is directly under the anterior termination of the latter. There are indications of moderate sized olfactory lobes in all cases, though these bodies are retained in none of the casts, the crura alone remaining. The temporal lobe is well defined in all cases. The hippocampal lobe is also quite prominent, being marked off from the sylvian gyrus by an ill-defined fissure. A prominent falx is noticeable between the hemispheres. There is a well-preserved representation of the decussation of the optic nerves in one specimen. The trigeminus nerve is prominent in all. The cerebellum is, in all cases, prominent and uncovered by the hemis pheres. Its longest vertical axis, continued through the subjacent pons, is equal to the corresponding axis of the hemispheres. In some cases there are indications that the middle lobe of the cerebellum was divided dorsally by a line at right angles to the dorsimeson. This division does not appear in all cases, probably owing to the superficial deposit of matrix. The middle cerebellar lobe is very prominent in all cases, presenting a smooth unconvoluted surface. The lateral lobes, though well defined, have shorter transverse and vertical axes than the middle lobe: like the latter they are unconvoluted. Prominent flocculi appear on the lateral surface of the epencephalon.[1]

A comparison with the brain of the pig does not bring to notice any very marked resemblances. The dorsal surface of the hemispheres is less elliptical, the temporal lobe being dorsally more prominent than in the pig. The cerebellum is relatively larger than the pig's, and is entirely uncovered by the hemispheres. Its median lobe is also more prominent than in the pig. The

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[1] Wilder, loc. cit., "Segment including cerebellum and subjacent parts."

flocculi and trigeminus nerves are quite pig-like. The casts have been reduced to three ill-defined classes, represented by Figs. 1, 2, 3, 4. Fig. 4 represents a class differing somewhat from that represented by Fig. 1. The general similarity of the main features of the casts has already been pointed out. It remains only to notice some of the distinctive characters of each class. Fig. 1 represents a class having its hemispheres marked by very prominent gyri. The median gyrus unites with the medilateral posteriorly. The anterior extremity of the temporal lobe is well marked. In Fig. 4 the transverse axis of the hemispheres, is relatively longer than in Fig 1, consequently the cerebrum presents a more oval appearance dorsally. A cast considerably larger than Fig. 1, but resembling it in outline, probably represents a larger animal of the same species. Fig. 2 represents a class having the longitudinal axis relatively larger than the classes represented by Figs. 1 and 4. The extension of the axis is mainly due to the forward growth of parts anterior to the temporal lobe. The median gyrus becomes continuous with the orbital. The median and medilateral gyri do not become completely continuous, being separated by a shallow fissure. Fig. 2 *a* represents a cast probably belonging to this class, which has had its prominent features somewhat obscured by a superficial deposit of matrix. The former is from Chalk Bluffs, Colorado, the latter from the Bad Lands, Dakota. Fig. 3 represents a well-defined class, where the longest longitudinal axis of the hemispheres was apparently somewhat shorter than the longest transverse axis. Its chief peculiarity consists in the marked divergence of the median and medilateral gyri from the meson posteriorly. This cast is moulded from the light-colored matrix found at Chalk Bluffs, Colorado. The darker-colored matrix, noticeable in other casts, is common in the Dakota Bad Lands. The casts probably represent several species of Oreodon, including *O. Culbertsonii*, *O. Major* and *O. Gracilis*. In the appended measurements, the cerebrum is measured dorsally, hence its longitudinal axis is not extended through the restored olfactory lobes.

Measurements.

Cast I. (Fig. 1.)	mm.
Longest longitudinal axis of cerebrum	47
" transverse " " "	42
" vertical " " "	31
" longitudinal " " cerebellum	25
" transverse " " "	27
" vertical " " "	32

Cast II. (Fig. 2.)	mm.
Longest longitudinal axis of cerebrum	45
" transverse " " "	39
" vertical " " "	34
" longitudinal " " cerebellum	34
" transverse " " "	30

The vertical axis of cerebellum in all cases is measured through the entire epencephalon.

Cast III. (Fig. 3.)	mm.
Longest longitudinal axis of cerebrum	38
" transverse " " "	40
" vertical " " "	23-4
" longitudinal " " cerebellum	20
" transverse " " "	22
" vertical " " "	24

POËBROTHERIUM.

Fig. 5 represents a specimen from the Bad Lands of Dakota. From the characters of some of the cranial bones found adherent to the cast, particularly the large tympanic bullæ, and from the general resemblance of the cast to the brain cast of Procamelus, described by Prof. Cope, the specimen has been classified as Poëbrotherium. A conference with Prof. Cope confirmed this view. The gyri, converging anteriorly and making acute angles with the meson posteriorly, indicate an ungulate type of brain. The configuration of the gyri is quite similar to that of Procamelus described by Prof. Cope in the United States Palæontological Report of the One Hundredth Meridian.[1] The median and medilateral run well forward. The latter is subdivided longitudinally throughout nearly its entire length. The median appears to be similarly subdivided posteriorly. The supersylvian and sylvian are united anteriorly and posteriorly. These gyri run further forward than in Procamelus. The dorsal surface of the cast of the brain cavity of Procamelus is more oval, there being less inward flexure anterior to the terminus of the supersylvian gyrus. The lateral features of the cast present a general likeness to the corresponding portions of the brain cast of Procamelus; as in the latter there is a well-defined hippocampal lobe, separated from the sylvian gyrus by a well-defined fissure. The cerebellum is not well preserved in the cast. Probably it resembled the cerebellum of Procamelus. The surfaces of the cerebellar lobes are smooth. The middle lobe is prominent. The flocculi at the sides of the epencephalon correspond to those of Procamelus. The lineal dimensions of the cast are about two thirds the corresponding dimensions of Procamelus. The latter, however, was a larger animal, consequently the increase of cerebral capacity does not, in this instance, imply a progressive increase with advancing evolution.

	mm.		mm.
Longest longitudinal axis of cerebrum	51	Longest longitudinal axis of cerebellum	21
" transverse " " "	42	" transverse " " "	36
" vertical " " "	36	" vertical " " "	30

CARNIVORA FISSIPEDIA.

ARCTOIDEA.

MEGENCEPHALON PRIMÆVUS.

The cast of which Fig. 6 is the representation was found in proximity to the remains of an Uintatherium near Henry's Fork. The matrix is the green sandstone of the Bridger Eocene.

[1] P. 338.

Compared with the smooth type of brain characteristic of many Eocene mammals the hemispheres of the cast are highly convoluted with sinuous longitudinal gyri. It is important to notice in this connection that as far back as the Bridger Eocene there are indications of large and small-brained types of mammals. In subsequent epochs the co-existence of these large and small-brained types became less marked owing to the disappearance of many representatives of the latter class. The preponderance which the large-brained [1] species acquired is well illustrated by the disappearance of the bunodont and the persistence of the lophodont Perissodactyla. The bunodont type represented by *Palæosyops* and allied forms possessed a small unconvoluted cerebrum with a large uncovered cerebellum and a prominent rhinencephalon, while the lophodont type represented by Aceratherium and Hyrachyus had a relatively larger cerebrum, marked by gyri and a smaller rhinencephalon.

By large-brained animals is understood those classes in which the ratio of the brain-weight to the body-weight is relatively large. In small-brained animals, on the other hand, this ratio is considerably less. The folding of the cerebral surface by bringing about a larger cerebral cortex is functionally equivalent to a larger unconvoluted cerebrum.

The brain of *Megencephalon primævus*, which the cast represents, belonged to one of the large-brained types of mammals found in the Bridger Eocene. A sacral vertebra found near the cast resembles the corresponding vertebra of the sea otter. The characters of the cast also suggest the brains of aquatic carnivora. The transverse axis of the cast is somewhat larger than its longitudinal axis, while the temporal lobe is ill-defined dorsally. The cerebellum is ill-defined, the ventral surface of the cast being very imperfect.

There are indications that the cerebellum was largely covered by the hemispheres. A depression originating in each hemisphere near the middle point of the dorsimeson (marked by a dotted line in the figure) extends backwards, diverging considerably. This depression possibly represents that part of the cerebellum left uncovered by the lateral divergence of the hemispheres. The broad transverse axis and the ill-defined temporal lobe giving the dorsal surface of the hemispheres an ellipsoidal appearance, suggest the brains of the seal, sea otter and dolphin. A comparison of the transverse with the longitudinal axis shows that the axes stand to each other in much the same ratio as do those of modern seals. The longitudinal axis is relatively shorter than the corresponding axis of the seal's brain, while it is relatively longer than the longitudinal axis of the dolphin's brain. The relative lengths of the axes agree

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[1] See Pal. Bull. No. I., this Museum, p. 20, Letter of Dr. Spitzka.

much more closely with those of the seal than with the corresponding dimensions of the dolphin's brain. The portion of the cerebrum posterior to the sylvian fissure is relatively large, thus indicating a further relationship with the seal. These correspondences, taken with the probability that the median portion of the cerebellum was exposed dorsally by the lateral divergence of the hemispheres and "with the absence of extensive transverse sulci" (Spitzka) seem to identify the specimen as a cast of the brain cavity of an Eocene otter or of some allied form. Three main gyri, most apparent on the right hemisphere, may serve for purposes of description. The course of each is very tortuous and ill-defined. The median, extending the length of the hemisphere, is bisected by a depression at right angles to the dorsimeson, as in the seal. This depression in the cast has probably been considerably worn and has consequently been made unduly prominent. It is difficult to determine how closely the remaining gyri correspond to those of the seal's brain, owing to their tortuous course. They appear, however, to bear a general resemblance to the gyri on the hemispheres of the seal. The temporal lobe was apparently extended somewhat farther forward than in modern seals.

Heretofore no remains of seals have been found in the Eocene, although intermediate forms between the seals and the Cetacea, Zeuglodon and Squalodon, are found in the American Eocene.

Measurements.

	mm.		mm.
Longest longitudinal axis of cerebrum......	46	Cerebellum, very ill-defined, greatest width probably.................................	25
" transverse " " "	52		

CYNOIDEA.

GALECYNUS GREGARIUS (?), COPE.

A small brain cast (Fig. 7) from the Miocene formation of the Dakota Bad Lands is probably the cast of the brain cavity of a small carnivore. The straight longitudinal convolutions and the characters of the cerebellum give support to this view. The triangular shape of the dorsal surface of the cerebrum, due to the narrowing of the hemispheres anteriorly, suggests the brains of the Canidæ. The outlines of the cast also resemble the brains of some of the Mustelidæ, particularly the weasel's brain. The triangular shape of the cerebrum and the longitudinal direction of the gyri might indicate a relationship to the rodents. But the gyri are more distinctly marked than in modern rodents. From what is known of the brains of Tertiary mammals it is hardly possible that rodents of that period should have possessed more highly convoluted brains than the

modern representatives of that order. From the features of the cast alone it would be rash to generalize; nevertheless it is very probable that the cast represents the brain of a species of Canidæ denominated *Galecynus gregarius* by Prof. Cope, inasmuch as representatives of that species are found in the Dakota Miocene. Judging from Prof. Cope's description, and from comparison with the brain cavity of a specimen in the E. M. Museum, there remains little doubt as to the identity of this cast. Its vertical axis appears to be somewhat shorter than the corresponding axis of the specimen examined. It is possible that this species of Canidæ combined some of the characters of the Mustelidæ, with more prominent canine characters. The special characters of the cast may be very briefly presented. There is no crucial fissure on the surface. The depressions of the hemispheres (marked by a dotted line in the figure) possibly mark the site of that fissure which has been obscured by the fracture of the cast at that point. The lateral fissure, separating the median and medilateral gyri, runs well forward. The medilateral and supersylvian gyri are separated by a fissure terminating above the sylvian fissure. The supersylvian and sylvian were probably separated by a continuous fissure extending from the origin of the olfactory crura over the sylvian fissure to the posterior part of the temporal lobe. The cerebellum is broad and convoluted, with a well-defined middle lobe.

Measurements.

	mm.		mm.
Longest longitudinal axis of cerebrum......	36	Longest longitudinal axis of cerebellum.....	13
" transverse " "	30	" transverse " "	23
" vertical " "	22	" vertical " "	15

AILUROIDEA.

HOPLOPHONEUS OREODONTIS (COPE).

The cast represented by Fig. 8, like the preceding, is from the Dakota Bad Lands. It differs from the preceding cast in size and in the configuration of the cerebral gyri. The well-defined gyri, running parallel with the dorsimeson, from which they diverge slightly anteriorly and posteriorly, indicate a carnivorous type of brain. There appears to be no crucial fissure. A slight depression of the median gyrus, a little anterior to the middle point, may represent a rudimentary crucial fissure. This, however, would place that fissure posterior to its present position. The same fissure may represent the prominent fissure formed at the junction of the median and medilateral gyri in the Felidæ. The blunted appearance of the hemispheres anteriorly, and the broad cerebellum with a somewhat prominent middle lobe, indicate affinities with the Ailuroidea. The gyri

on the surface of the hemispheres are less tortuous than in modern Felidæ. The median and medilateral are separated throughout their entire length. The supersylvian and sylvian gyri are more distinct than in the modern Felidæ. The former is subdivided by a longitudinal fissure, which suggests a like fissure in the cat's brain.

The lateral aspect of the cerebrum is very similar to the cerebrum of the cat similarly viewed. The relatively long vertical axis through the temporal lobe is a marked feline feature. The cerebellum is partly covered by the hemispheres. Its middle lobe is somewhat more distinct than in modern Felidæ. The lobes of the cerebellum were probably smooth. The remains of several species of Felidæ have been found in the Bad Lands. The specimen may be provisionally classified as *Hoplophoneus Oreodontis*. A comparison of the cast with a skull and cast of Hoplophoneus at the Philadelphia Museum leaves little doubt on this point.

Measurements.

	mm.		mm.
Longest longitudinal axis of cerebrum......	43	Longest longitudinal axis of cerebellum.....	18
" transverse " "	42	" transverse " "	36
" vertical " "	39	" vertical " "	30

CREODONTA.

LEPTICTIS (LEIDY).

Fig. 9 represents the brain cast of a small Miocene mammal; portions of the skull found adherent to the cast, served to identify it as the brain cast of a small Creodont, described by Dr. Leidy as Leptictis. The most characteristic features of the skull are the prominent ridges extending along the inner border of the temporal fossæ. These ridges, together with the size and shape of the skull, and the character of the teeth, are sufficient to establish the identity of the cast. It is difficult to compare the cast with the brains of any specific group, owing to the generalized characters of Creodonts. They probably combined the characters of the Marsupials and Carnivora with some insectivorous characters. Hyænodon, a representative Creodont, closely resembles the marsupial Thylacynus. Hyænodon is also plantigrade and has a third trochanter on the femur. The cast indicates a simple type of brain, comparable with the brains of existing rodents. Its ventral surface is very incomplete. Dorsally the cerebrum is triangular in outline. There is a single ill-defined longitudinal fissure on each hemisphere, resembling a like fissure noticeable on the cerebra of some rodents.

There appear to be no indications of other fissures on the cerebral surface of the cast. The cerebellum is large, smooth and

uncovered by the hemispheres. The cerebellar lobes are not distinct, the greater part of the cerebellum probably representing the middle lobe of higher mammals. The largest vertical cerebellar axis, measured, as in other cases, through the entire epencephalon, is somewhat longer than the corresponding axis of the cerebrum. The cranial bones suggest the size of the animal. Though probably it was as large as the weasel, the cast shows the animal's brain to have been somewhat smaller than the squirrel's brain. The single longitudinal fissure on the hemisphere apparently corresponds to a similar fissure on the cerebrum of the hedgehog. This correspondence may be of importance as indicating some insectivorous characters.

Measurements.

	mm.		mm.
Longest longitudinal axis of cerebrum,	19.	Longest longitudinal axis of cerebellum,	13.
" transverse " " "	21.	" transverse " " "	+
" vertical " " "	17.	" vertical " " "	17.

In most specimens the ventral surfaces were incomplete, consequently descriptions of parts pertaining to those surfaces have generally been omitted.

CONCLUSIONS.

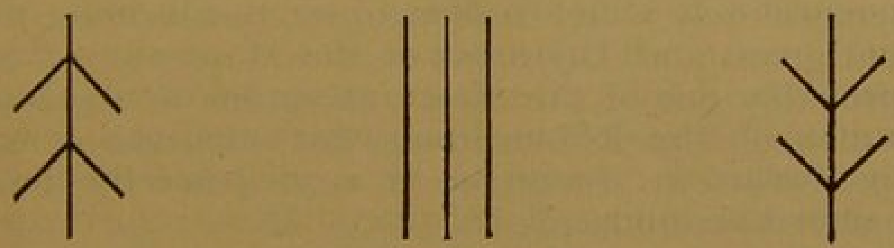
In conclusion it seems proper to point out some phases of encephalic growth which the casts described suggest. When comparison was possible, the casts, after making due allowances for the minor features of the brain which cannot be well represented by a cast, were found to be smaller and less highly convoluted than the brains of existing mammals of the same size and order. The casts of Oreodon were much smaller than the pig's brain: making deductions for the smaller size of Oreodon, which the numerous remains of its skeleton amply prove, it appears that the brain of the pig is relatively larger. The brain cast of Poëbrotherium does not admit of any exact comparison with the brains of existing Camelidæ.

The brain cast of Megencephalon, tho smaller than the sea otter's brain, does not admit of any exact comparison with the brain of the otter, in the absence of the cranial bones. The brain cast of Hoplophoneus indicates a relatively small-sized brain. Tho probably as large as a panther, this animal had a brain not much larger than a cat.

As before intimated, the brain of Leptictis must have been small considering the size of the animal. In all the casts where it is distinct, the cerebellum is nearly or entirely uncovered by the hemispheres. Moreover the cerebellum is, in most instances, of a relatively large size. Consequently, the evidence presented by the specimens described confirms the statement of Prof. Marsh, that most Tertiary Mammals had small brains, and that encephalic growth has been mainly confined to cerebral growth.

It seems probable that the primitive gyri on the dorsal surface of the hemispheres were ill-defined, and of the longitudinal type, running parallel to the dorsimeson with little flexure. The fact that the brains of Rodents, Edentates and Insectivora generally present this type of gyri, is evidence that the least differentiated gyri were arranged as stated. The brain casts of the Carnivora described, with the exception of *Megencephalon primævus*, exhibit nearly straight longitudinal gyri, not diverging from the meson anteriorly or posteriorly, as do the corresponding gyri on the cerebra of modern Carnivora. Moreover, the transverse crucial fissure prominent in existing Carnivora, if present at all, must have been quite rudimentary.

The evidence seems to sanction the view that transverse gyri were subsequent to longitudinal gyri, in order of appearance. The primitive longitudinal gyri may be supposed to be represented by similar gyri in the hemispheres of the lower Mammalia, and in a modified form by the gyri on the hemispheres of modern Carnivora. In the case of Ungulates, a modification of this primitive form of gyri may be assumed to have been effected by anterior convergence. In the history of Primates, a posterior convergence of the primitive dorsal gyri is also supposable.



1. Ungulate type. 2. Primitive type. 3. Primate type.

The large size of the cerebellum in fossil mammals has been pointed out. However, it does not necessarily follow from this that there has not been an increase of cerebellar cortex effected, as in the cerebrum, by the folding of the surface. The most noticeable feature of the cerebellum of the casts examined is the prominent middle lobe. Existing mammals of the lower orders possess a similarly configured cerebellum. In man the middle lobe is reduced to a minimum, the lateral lobes comprising the greater part of the cerebellum. It seems probable that there has been a decrease in the size of the middle lobe and a concomitant increase of the lateral cerebellar lobes with progressive evolution.

Moreover, the supposition that the middle cerebellar lobe of the Mammalia was primarily the largest cerebellar lobe is supported by embryological evidence, that lobe being prominent in the embryonic phases of the higher Mammalia, where it subsequently becomes smaller than the lateral lobes.

IV.

TWO NEW EOCENE LOPHIODONTS.

W. B. SCOTT.

I.—DESMATOTHERIUM GUYOTII. (*Gen. et spec. nov.*)

This interesting new form (Plate VIII, Figs. 1–3) is from the Bridger Eocene of Wyoming Territory, and represents a Lophiodont genus closely allied to *Hyrachyus*, but forming a link between that genus and *Tapiravus* of the Miocene. It therefore is very probably one of the direct ancestors of the Tapirs, and possibly also of the Rhinoceroses, but until the construction of the premolars in *Amynodon* is more perfectly known this point must remain undecided.

The specimen preserved in the Princeton collection exhibits the entire upper dentition, lacking the incisors only. The crown of the first premolar on each side is so broken as not to admit of description.

Definition of the Genus. Lophiodonts closely allied to *Hyrachyus*, having the molar teeth constructed exactly as in that genus, but differing from it in the pattern of the third and fourth upper premolars, which have two internal cusps instead of one. Dental formula:

$$i. \frac{?-?}{?-?}\ c. \frac{1-1}{?-?}\ pm. \frac{4-4}{?-?}\ m. \frac{3-3}{?-?}.$$

There is a long diastema between the canine and the first premolar.

Definition of the Species. The animal is of a size intermediate between *Hyrachyus agrarius* and *H. nanus*. The internal cusps of the third and fourth upper premolars are closely approximated and the crests low. The postero-internal cusp of the fourth is very small and situated somewhat exterior to the

antero-internal cusp. The external accessory buttress is well developed on the teeth from the third premolar backward, and is indicated on the second. The cingulum of the last molar is raised into a tubercle on the anterior face of the crown.[1]

To describe the specimen somewhat more in detail. The first premolar is very small and evidently simple; of its crown nothing further can be said, as it is badly broken. The tooth was inserted by two fangs.

The second premolar is not essentially different from the corresponding tooth in *Hyrachyus;* the external face presents, however, a more nearly quadrate outline; the anterior edge is more nearly vertical and the antero-external buttress more distinctly marked. The external face is separated into two lobes by a groove deeper and more decided than in *Hyrachyus.* There is but one internal cusp, which sends off one very obscure anterior crest; this does not reach the external wall, but is separated from it by a longitudinal valley. The cingulum is faint, and is present only on the front and rear faces of the tooth.

The third premolar is very different from that of *Hyrachyus* in showing the molar pattern. The antero-external buttress is much larger than in that genus, being as well developed as in the molars. There are two internal cusps, and from each of them there proceeds a transverse crest to the external lobes. Of these crests the anterior is much the stronger. The two internal cusps are closely approximated, being separate only at their apices, and for the remainder of their height marked off from each other only by a deep groove. By this arrangement the median valley of the tooth does not open directly inwards, as it does in the molars.

The fourth premolar is larger than the third, and at first sight quite like the fourth premolar of *Hyrachyus.* But a closer examination reveals important differences. There are, as in the third premolar, two internal cusps, but this division is not so plain, as the posterior one is very small, and the posterior crest joins both it and the anterior cusp. The valley is therefore enclosed on all sides. The two external lobes in the three last premolars are of similar size and shape, thus differing from the molars. It cannot be said, therefore, that the third and fourth premolars are exactly of the molar pattern, though the beginning of the transformation is here very evident.

Besides the differences already mentioned between the last premolars of *Hyrachyus* and *Desmatotherium* there is another of less importance. In the former this tooth has the cingulum raised into a strong postero-external buttress, as well as into an antero-external one, thus giving the external face of the crown

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[1] This species is respectfully dedicated to my revered friend and teacher, Prof. Arnold Guyot.

a four-lobed appearance.[1] In the latter genus this is not at all well marked; it is about as in the molars of both genera.

The true molars of *Desmatotherium* are very similar indeed to those of *Hyrachyus*, but with some differences of detail. This genus agrees with the Lophiodonts and differs from the Tapirs in having the two external cusps somewhat unlike each other, the anterior one being convex and somewhat longer, the posterior one concave. In the Tapir, on the other hand, the two cusps are both convex and of similar size; the transverse crests are also less oblique, and the external wall of the tooth is not continued quite so far behind the posterior crest as in the Lophiodonts. *Desmatotherium* resembles the Lophiodonts in the type of its molars much more closely than it does the Tapirs, but perhaps the beginnings of change towards the latter may be detected. In the first molar the two external cusps are somewhat more alike than in *Hyrachyus*, and the external wall is not continued quite so far behind the posterior crest, so that the posterior valley is not so deep and has a somewhat different shape; the direction of the transverse crests is almost exactly the same. The antero-external buttress of the molars is of greater size relatively and more closely approximated to the antero-external lobe than in *Hyrachyus*, and more like the arrangement in the Tapir.

The cingulum is not very distinct except on the last molar. On the anterior face of this tooth the middle of the cingulum rises up to form a small prominence not seen in any of the species of *Hyrachyus* in our collection.

Through the whole series of molar teeth there is a progressive increase of size as we pass backwards, the first premolar being the smallest and the last molar the largest of the series.

The canines (Pl. VIII, Fig. 3) are very like the same teeth in *Hyrachyus*, though perhaps a trifle smaller. They are curved and provided with stout fangs. In direction they pass somewhat outwards as well as downwards. In section they are oval and depressed, the long axis being directed from side to side.

Measurements.

	M.
Length of entire molar series	.079
" " premolar series	.036
" " true molar series	.043
Fore and aft diameter of 1st *premolar*	.005
Transverse " " " "	.003
Fore and aft " " 2d "	.008
Transverse " " " "	.010
Fore and aft " " 3d "	.011
Transverse " " " "	.013
Fore and aft " " 4th "	.012
Transverse diameter of 4th *premolar*	.014
Fore and aft " " 1st *molar*	.013
Transverse " " " "	.016
Fore and aft " " 2d "	.015
Transverse " " " "	.016
Fore and aft " " 3d "	.017
Transverse " " " "	.017
Length of diastema between canine and premolars	.022

The especial interest of this new genus is morphological, and

[1] See Leidy, Contrib. to Ext. Vert. Fauna of the West, Plate IV, Figs. 9 and 10.

for the light which it throws upon the steps by which the Eocene Lophiodonts gave rise to the modern Tapirs. In order to understand this transformation it will be necessary to make a comparison between the extremes of the series and observe how the modern Tapir differs from such a form as *Hyrachyus*. The latter was an animal extremely like the Tapir in general appearance and in the broad characters of skull, skeleton and dentition, but at the same time displaying such differences from it as to necessitate placing it in another family.

(1) The skeleton of *Hyrachyus* a sa whole was lighter, the processes for muscular attachment less developed, and the limbs longer and more slender.

(2) The cranium was relatively smaller, the sagittal crest longer and the forehead less rounded, owing to the very small size of the frontal sinus.

(3) The nasals were probably longer and the narial opening not nearly so large.

(4) The upper canine was as large as the lower, which was erect.

(5) The premolars were all of a simpler pattern than the molars, having only one internal cusp.

(6) In the molars the two external cusps were of different shape, the anterior being convex and the posterior concave, while in the Tapir they are both convex.

(7) The antero-external buttress was not so closely applied to the neighboring external cusp.

(8) The neck was somewhat longer.

(9) The scapula was larger relatively.[1]

(10) The ilium had a much longer plate.[1]

(11) The limbs were longer and more slender proportionally.

(12) The radius was less expanded distally, and never co-ossified with the ulna.

(13) The pisiform articulated with the ulna by a much smaller face, and covered less of the cuneiform.

(14) The magnum was very much smaller, and the unciform somewhat larger.

(15) The metacarpals were longer and more slender; the median one not so stout; and the lateral ones, especially the fifth, better developed.

(16) The astragalus and calcaneum were longer and narrower.

(17) The metatarsals show the same differences from the modern forms as do the metacarpals.

It will be at once apparent that most of the changes which have taken place in this line are comparatively insignificant and easily intelligible. It is only in the dentition that the successive

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[1] See Cope, Sixth Ann. Rep. U. S. Geolog. Survey of the Territories, 1872, p. 603.

steps can be followed by means of the material which has as yet been discovered, yet we cannot doubt that the fresh material which is constantly brought to light will confirm the determinations made from the successive modifications of the teeth.

The molars of *Hyrachyus* are strikingly like those of the Tapir, showing even the small accessory ridge which projects from the external wall into the median valley, and the antero-external buttress of the crown. There is a difference, however, in the fact that in the molar tooth of the Eocene type the antero-external cusp is convex, while the posterior one is concave. If, as has been suggested by Prof. Cope, and as is extremely probable,[1] the Lophiodont form of dentition is a modification of the *Palæosyops* type in which the external cusps are both concave, this inequality has nothing surprising in it. Two kinds of Perissodactyl molars seem to be derived from the Lophiodont type; one is that of the Rhinoceros and *Hyracodon* series (see the first article of this Bulletin), the other the Tapiroid type. The first step towards the latter series is seen in *Desmatotherium*, where the inequality of the external cusps of the first molar is less marked and where the premolars are beginning to assume the molar pattern. This transformation has hardly gone far enough for us to say that they are alike, yet the third and fourth premolars present all the elements of the molar tooth.

In the Lower Miocene the genus *Tapiravus*[2] of Prof. Marsh carries the modification further still in that the fourth premolar is exactly like the molars. He does not state anything as to the equality or otherwise of the external cusps. *Anchisodon* (Cope[3]) has the third and fourth premolars both on the molar pattern, and Prof. Cope includes this genus among the family *Tapiridæ*. The place of *Desmatotherium* in the line of the Tapirs seems thus to be perfectly clear. It represents the first step of the modifications which gradually metamorphosed *Hyrachyus* into *Tapirus*. That both of these genera belong in the series of direct ancestors of the Tapir seems at present hardly open to question.

The relations of *Desmatotherium* to the Rhinoceros line are by no means so evident. It would not be surprising if future discoveries were to show that this genus, and not *Hyrachyus*, were the common starting-point of the Rhinoceros and Tapir lines, and yet from the evidence which we have at present this seems hardly probable. *Amynodon* appears to have simpler premolars than *Desmatotherium*, and even if it should turn out that in this form the premolars have two internal cusps, yet the stratigraphical evidence is that *Orthocynodon* is an older form

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[1] Cope, Journ. Acad. Nat. Sci. Phila., 1874, pp. 13, 14.
[2] Am. Journ. Sci. and Arts, 3d ser., vol. xiv. p. 252.
[3] Am. Nat., 1879, p. 270.

than *Desmatotherium.* This latter objection may of course at any time be removed, and should be allowed only a negative value.

We have seen in the first paper of this Bulletin that probably the first change from *Hyrachyus* towards the Rhinoceros lines was in the transformation of the molar teeth to the characteristic Rhinoceros pattern, especially by the great reduction of the antero-external cusp. In *Desmatotherium* what little difference from the molars of *Hyrachyus* there is, points rather to an equalization of the cusps, the great change being in the character of the premolar teeth.

Taking, therefore, everything into consideration, it must be admitted that the tendency of our knowledge at present is to place this new Lophiodont only in the ancestral line of the Tapirs, although, as I have already said, it may very well happen that future investigations may prove that it also stands in a similar relation to the Rhinoceroses.

II.—DILOPHODON MINUSCULUS. (*Gen. et spec. nov.*)

(Plate V, Fig. 4).

This genus is established on a portion of the lower jaw, embracing the right ramus with the entire molar series and the symphysis, but lacking the canines and incisors. The specimen was found in the Bridger Eocene of Wyoming Territory.

Definition of the Genus. Lophiodonts closely allied to *Hyrachyus*, having the last lower molar with two transverse crests, and a diastema between the canines and molar series, but with only three premolars in the lower jaw.

Definition of the Species. (1) *Dilophodon* (*Hyrachyus*) *nanus*, Leidy. Last lower molar with a small posterior heel; diastema between canines and molars very long.

(2) *D. minusculus*, Scott. Animals considerably smaller than the foregoing species; last lower molar without any trace of a posterior heel; diastema very short.

It was with considerable hesitation that this genus was formed, for such a character as the absence of the first lower premolar is not always a safe criterion, but its constancy even in young specimens, and its occurrence in two such entirely distinct species, made it evident that this is not merely an uncertain variation. If it be thus a constant character, there can be no question that it has a generic value.

The specimen before us is one of the smallest of the known Lophiodonts. It was from an animal barely adult, as the first molar is but slightly worn, and the crown of the last molar is not yet protruded to quite its full height.

The jaw is shaped like that of *Hyrachyus*, rather deep and with a thickened alveolar border. Behind the molars the ramus becomes very thin and is extended far back. The short diastema indicates rather a short-headed animal. The symphysis is very narrow and apparently quite short, so that the canines and incisors must have been closely crowded together; the jaw is broken off close to the roots of the former. The jaw is much contracted at the symphysis, though it was not very wide in any part.

There are three small mental foramina, which occupy a very similar position to those in *D. nanus*, but owing to the shortness of the diastema they are brought closer together and lie all in the same straight line; the posterior one lies just below the space between the first two premolars (second and third of the full series). These foramina are very small, much more so than in *D. nanus* (see Leidy, Contrib. to Ext. Vert. Fauna of West, Pl. XXVI, Fig. 11). At the diastema the alveolus is contracted to a very thin edge, which curves down and then up again to the insertion of the canine.

Dentition. As far as can be judged from the broken roots, the incisors are like those of *Hyrachyus*, both in number, shape and size. The roots are much compressed and the crowns are apparently somewhat procumbent. The canines are very small indeed, though this may be a characteristic of the sex of the animal rather than of the species.

There is no trace whatever of the presence of the small first premolar. As already stated, the animal was barely adult, and so the absence of this tooth cannot be due to age.

The second premolar (first in this genus) is a small tooth inserted by two fangs. It is very similar to the corresponding tooth in *Hyrachyus*, but has the anterior fossa a little more distinct.

The third premolar shows no differences from that of *Hyrachyus*.

The fourth premolar is rather more like the molars than is the case in *Hyrachyus*, in the somewhat greater elevation of the posterior crest. All the premolars, however, as in that genus, have the anterior lobe considerably higher than the posterior, but the elements of the molar teeth are present in the third and fourth at least, and it would require only a very slight change of proportion to reduce these teeth to the molar pattern.

The molars of the specimen before us call for no special description, as they are precisely like those of *Hyrachyus*. The last one is the largest, and has no trace of the heel which is to be seen in *D. nanus*, far less of the third lobe which is found in *Lophiodon* and *Helaletes*.

Measurements.

	M.		M.
Length of entire molar series	.045	Transverse diameter of 1st molar	.006
Length of premolar series	.019	Fore and aft " " 2d "	.009
Length of true molar series	.026	Transverse " " " "	.006
Fore and aft diameter of 1st premolar	.005	Fore and aft " " 3d "	.009
Transverse " " " "	.004	Transverse " " " "	.007
Fore and aft " " 2d "	.007	Diameter of canine at base	.003
Transverse " " " "	.005	Length of diastema	.014
Fore and aft " " 3d "	.007	Breadth of symphysis at canines	.008
Transverse " " " "	.006	Depth of ramus beneath 1st premolar	.013
Fore and aft " " 1st molar	.008	" " " " 3d molar	.017

The following systematic table of the genera of the *Lophiodontidæ* may be of some value in showing the various modifications which this group presents.

LOPHIODONTIDÆ.[1]

Perissodactyls having the external cusps of the upper molars of different shape from each other; upper and lower molars supporting transverse crests. Molars and premolars unlike.

I. Anterior digits three. *Triplopus.*
II. Anterior digits four.
  1. Nasals supporting a pair of rudimentary horns. *Colonoceras.*
  2. Nasals hornless.
    a. No diastema between canines and premolars. Last lower molar with three lobes. *Helaletes.*
    b. A diastema between canines and premolars.
      (1) Upper premolars with one internal cusp.
        (*a*) Transverse crests of lower molars connected by oblique crests. *Pachynolophus.*
        (*b*) No oblique crests in lower molars.
          aa. Last lower molar tri-lobed. *Lophiodon.*
          bb. Last lower molar bi-lobed.
            A. Molar series $\frac{7}{7}$. *Hyrachyus.*
            B. Molar series $\frac{7}{6}$. *Dilophodon.*
      (2) Third and fourth upper premolars with two internal cusps. *Desmatotherium.*

I have not included *Tapirulus* in the above list, because Gervais's figure and description give no reason for separating it from *Lophiodon.* Prof. Cope can hardly be right in considering *Helaletes* a synonym of this genus.

[1] This definition modified from Cope, Bull. U. S. Geolog. Survey, vol. v. no. 2, p. 228.

EXPLANATION OF THE PLATES.

PLATE V. ORTHOCYNODON ANTIQUUS.

Fig. 1. Side view of skull, restored.
Fig. 2. Crowns of the superior molar series.
Fig. 3. Crowns of inferior molar series.
Fig. 4. Crowns of median lower incisors.
Skull one half natural size, other figures two thirds natural size.

PLATE VI. ACHÆNODON ROBUSTUS.

Fig. 1. Side view of the skull, restored.
Fig. 2. Crowns of upper canine and molar series.
Fig. 3. Crowns of lower canine and molar series.
Figures one half natural size.

PLATE VII.

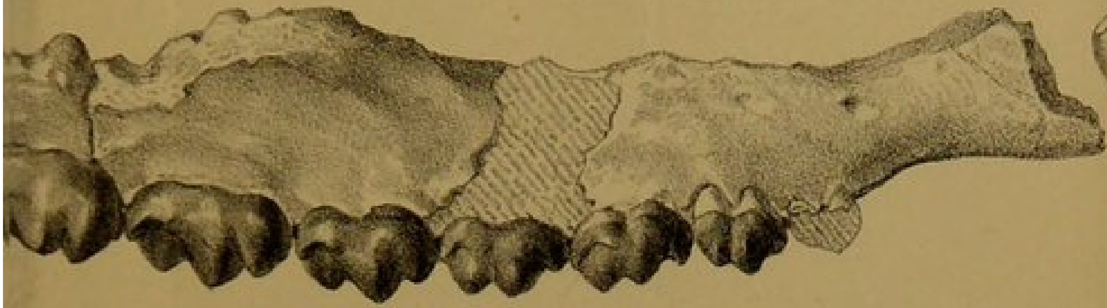
Fig. 1. Side view of cranial cast of OREODON. (Class I.)
Fig. 2. Dorsal view of cranial cast of OREODON. (Class II.)
Fig. 2*a*. Dorsal view of cranial cast of OREODON.
Fig. 3. Dorsal view of cranial cast of OREODON. (Class III.)
Fig. 4. Dorsal view of cranial cast of OREODON.
Fig. 5. Dorsal view of cranial cast of POEBROTHERIUM.
Fig. 6. Dorsal view of cranial cast of MEGENCEPHALON PRIMÆVUS.
Fig. 7. Dorsal view of cranial cast of GALECYNUS GREGARIUS (?).
Fig. 7*a*. Lateral view of the same.
Fig. 8. Dorsal view of cranial cast of HOPLOPHONEUS OREODONTIS.
Fig. 8*a*. Lateral view of the same.
Fig. 9. Dorsal view of cranial cast of LEPTICTIS.
m, median gyrus; *l*, lateral gyrus; *ss*, supersylvian gyrus; *s*, sylvian gyrus; *o*, orbital gyrus.
Figures natural size.

PLATE VIII.

Fig. 1. Right superior maxillary of DESMATOTHERIUM GUYOTII.
Fig. 2. Fang of right superior canine of the same.
Fig. 3. Crowns of superior molar series of the same.
Fig. 4. Right mandibular ramus of DILOPHODON MINUSCULUS.
Figures natural size.

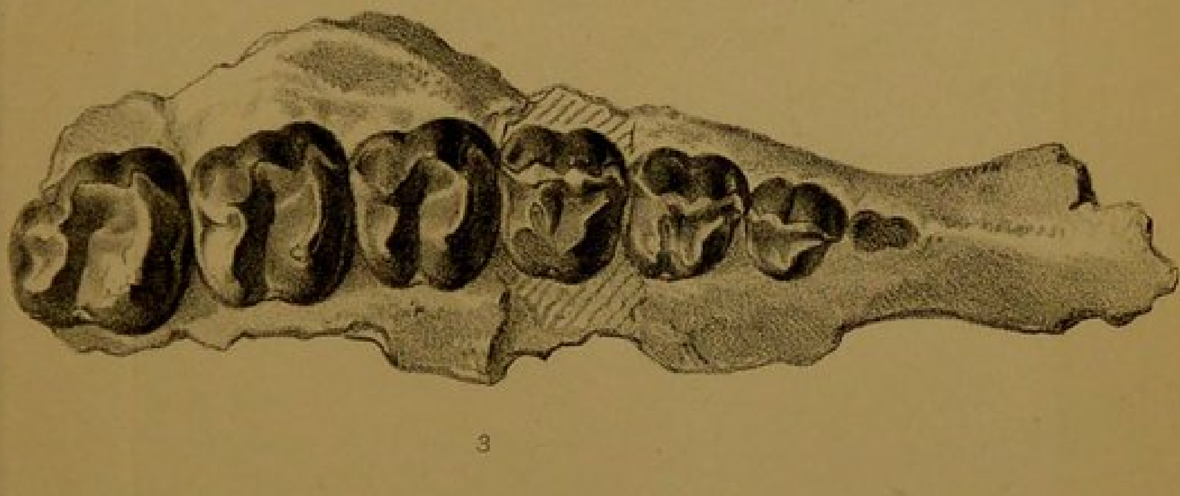
T. Sinclair & Son, Lith. Phila.

4. OREODON. 5. POEBROTHERIUM. 6. MEGENCEPHALON PRIMAEVUS. 7. GALECYNUS GREGARIUS.
8. HOPLOPHONEUS OREODONTIS. 9. LEPTICTIS.

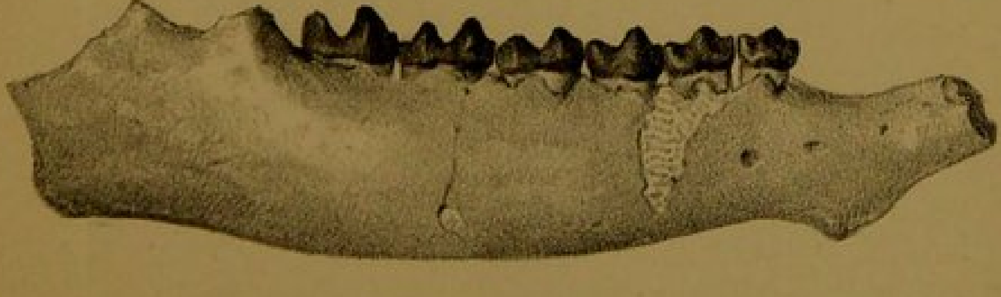


1

2



3



4

T. Sinclair & So