Topography compensates deficiency or excess in isostatic shell.

Mr. R. D. Oldham, in discussing a paper[5] on isostasy presented before the Royal Geographic Society by Col. Burrard, emphasized the importance of stating clearly whether a mountain is compensated for by the deficiency of material in the column under it, or whether the mountain is a compensation of the light material of the column. Geodesists have spoken of compensating deficiencies of material under the continents and compensating excesses of material under the oceans, but it is the writer's belief that the mountain masses and the deficiency of matter in the oceans compensate the abnormal conditions of density which exist in the columns under them.

[5] A Brief Review of the evidence on which the theory of isostasy is based. Geographic Journal, July, 1920, London.

Art. II.—*New Amynodonts in the Marsh Collection*; by Edward L. Troxell.

[Contributions from the Othniel Charles Marsh Publication Fund, Peabody Museum, Yale University, New Haven, Conn.]

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The Amynodontidæ.

Summary of Species and Relationships.

Orthocynodon Scott and Osborn (1882, p. 223), *Amynodon* Marsh (1877, p. 251), and *Metamynodon* Scott and Osborn (1887, p. 164) constitute a group of rhinoceros-like ungulates found in America alone. Authors have placed *Cadurcotherium* in the family Amynodontidæ, apparently on the basis of the great premolar reduction, but this seems wholly inharmonious when we judge this genus from the figures of its teeth (Abel 1914, p. 239).

Metamynodon planifrons Scott and Osborn and *M. rex*, sp. nov., come from the lower *Oreodon* beds, from a zone of river sandstones characterized by and named from the genus. Only two of these interesting specimens have been described and but few skulls are known to exist. The holotype of *M. planifrons* is in the Museum of Comparative Zoology at Harvard University; it consists of a skull and jaws. A fine complete skeleton in the American Museum of Natural History has been fully described by Osborn (1898, pp. 80-94).

The genus *Amynodon* is better known, because it is represented by several species: *A. (Orthocynodon) antiquus* (Scott and Osborn) is found in the Middle Eocene or Washakie; *A. advenus* (Marsh) and *A. intermedius* Scott and Osborn, together with *A. erectus*, sp. nov., represent the Uinta beds of the Upper Eocene, and are in general more advanced in their evolution. The Yale specimens come from the region of White River, Utah.

[1] This is the first of a series of four articles on the rhinoceroses in the Marsh Collection; the three others deal in turn with *Hyracodon*, *Cœnopus*, and *Diceratherium*.

A. antiquus may be distinctly separated from the others, perhaps subgenerically, by the presence of both upper and lower functional first premolars, and by a marked difference in the general proportions of the teeth. The new species, *A. erectus,* is small and primitive, and in this respect approaches *A. antiquus,* but it has lost all trace of the first premolars and is of a later geological horizon. *A. intermedius,* the largest and most progressive of the species, resembles *Metamynodon* in the form of its canines and molars and approaches it in the size of the teeth, and in the stage of the premolar reduction also, where the premolar series measures half the molar length.

In progressing to the state of *Metamynodon,* an undoubted lineal successor, besides the slight further reduction of the premolars, we note the gradual lengthening of the skull behind the orbits, the widening of the molar teeth, the tendency toward complicated folds on the premolars, the increase in the size of the canines, the closing of the external auditory meatus below, and the general crowding and concentrating of the hinder part of the skull near the condyles or fulcrum, this last made necessary by the enormous increase in weight of the skull as a whole.

Adaptations to Physical Environment and to Feeding.

Most of the characters which distinguish these animals from the true rhinoceroses are thought by Osborn, Scott, and others to be a response to the needs of a semi-aquatic life. This is borne out especially by the observations on (1) the posture of the naso-maxillary opening, governed by the short nasals; (2) the position and form of the posterior nares; (3) the high, anterior position of the orbits; (4) the broad, spreading feet and their ability to fold backward; and (5) the great increase in size.

The naso-maxillary opening, or anterior nares, which depends upon and at the same time determines the form of the nostrils, taken together with certain features to be discussed later, suggests a prehensile, or very mobile lip such as one sees in the hippopotamus and other water animals. The depth and position of the posterior nares seem to facilitate breathing, by making a closer connection between the larynx and the nasal passages when the mouth is full of food or water; and further, they prevent the entrance of foreign substances, water, etc., into the larynx and windpipe while the mouth is open under water as in the act of gathering food.

An intimate connection of the epiglottis with the pharynx, as enclosed by the soft palate, is seen in the modern horse, where no passage of air is possible through the mouth in ordinary breathing. In this recent animal, it is thought to be a provision against breathing the dust from the grasses which constitute a greater part of its food. There is a resemblance in the form of this opening in the amynodonts and in the horse.

A further adaptation to a watery habitat is seen in the forward and high position of the orbits, which serves to keep the periscopic eyes out of the water for swimming or for observation while hiding; this finds its greatest development in *Hippopotamus,* in which the orbits actually rise above the plane of the face, and here also, as well as in *Metamynodon,* we find the broad spreading feet suited for walking on the softer ground near and in rivers and lakes—feet which are so constructed that the toes fold together backward as they are lifted and carried forward through the resisting water.

In speaking of the hippopotamus, Roosevelt and Heller say that the semi-aquatic habits have favored its development to an enormous bulk. This is no doubt true of *Metamynodon* also, and while locomotion would be difficult and clumsy on the land, it would be greatly facilitated by the buoyancy of water even if the beast were only partly submerged.

In both the genera of the Amynodontidæ the skulls show fossæ in the roof of the mouth, the purpose of which is problematical; but together with the deep antorbital depressions, they certainly constricted the nasal passages to a considerable degree and must have interfered with the organs of smell—of minor importance to an aquatic beast.

The following points may be interpreted as evidence of a prehensile lip at least in *Metamynodon:* (1) the roughened supra-orbital ridges, together with the conspicuous tubercles just in front of the eyes, and (2) the large cheek depressions, possibly indicative of large face muscles; (3) the moderately large infra-orbital foramina, doubled in the holotype of *A. erectus,* and required in order to furnish plentiful nourishment and nerves to the facial organs; and finally (4) the nature of the narial opening which, especially in *Metamynodon,* is triangular in form, broad above and constricted below, and situated well back on the maxillaries, due to the abbreviated nasal bones.

We may judge further of the living conditions of the Amynodontidæ by the character of the teeth. The canines and molars have developed with the skull and are larger than those of any other rhinoceros of the period, but the incisors and premolars have not kept pace and are scarcely larger than in *Amynodon,* showing but slight need for cutting teeth in these animals. The upper canines of *Metamynodon* and of *A. intermedius* were strongly procumbent and diverging; they were not erect in the jaw like the canines of *Archæotherium.*

The molars are broad and flat and in their use must have been comparable to those of an elephant, serving to grind up the food secured by the canines; this may have consisted of bark, tuberous roots, nuts, or leaves, gathered near the aquatic haunts, in the mastication of which the molars were used, leaving no need for premolars of the cutting type.

There seems to be little wear relatively on the narrow premolars; most of it comes on the middle of the cheek series, on M^1 especially. There is naturally less wear on M^3 which appears last, though on this molar one sees the vestigial extension of the ectoloph beyond its junction with the metaloph, which serves to prolong the period of usefulness of the tooth by furnishing a longer grinding surface.

In comparing these metamynodonts with the other groups of rhinoceroses of the period, we see that *Cænopus* and *Diceratherium* developed their molars more like the horses, i. e., for grazing, had sharper edges on the ectoloph for cutting the food, and the premolars were much more advanced and more molariform than in any of the amynodonts.

Description of New Species.

Metamynodon rex, sp. nov.

(Figs. 1, 2.)

Holotype, Cat. No. 10274, Y. P. M. Lower Oligocene (*Metamynodon* zone), Pine Ridge Agency, South Dakota.

This fine specimen was purchased from Mr. C. H. Little

of South Dakota in 1889 by Professor Marsh; only recently has it been freed from the stony matrix and identified.

Skull characters.—The malar-temporal suture begins in the orbit; the zygomatic arch is concave internally in both directions and is very broad. The strong sagittal crest rises an inch or more above the cranium. The posterior nares lie entirely behind the last molar, with the opening very deep and well guarded by the broad pterygoids. The wide spacious articular glenoid surface extends onto the heavy postglenoid process, which curves forward and away from the paramastoid to which it is closely joined. The basicranial angle is large, a progressive character. The roof of the mouth is arched into a deep fossa between the premolars. There are deep cheek depressions, but they are restricted in area. The nasal bones are short.

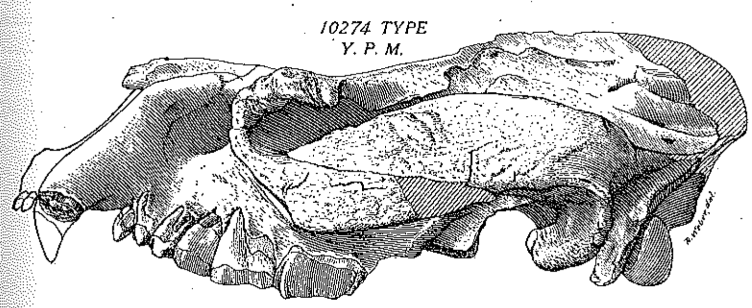

Fig. 1.—*Metamynodon rex,* sp. nov. Holotype. Side view of skull of the ponderous aquatic rhinoceros. Note heavy zygomatic arch, deep facial pit, strong outward curving canine (restored), and short face. × 1/6.

Dentition.—The incisor teeth, absent here, are known to be small in the type of *M. planifrons.* A diastema of 3 mm. separates the canine from P^2. P^1 is obsolete. P^2 forms an irregular pentagon; it is probably three-rooted, and is made up of crests and ridges like the other premolars, but appears in its natural posture to have been rotated through an angle of 80 or 90 degrees; thus the protoloph and metaloph extend directly backward instead of transversely.

P^3 is broad transversely and short antero-posteriorly, the diameters being 31 by 21 mm. The ectoloph is broad and in the present state of wear occupies about half of the surface of the tooth; the metaloph is very narrow, joins the protoloph through the deuterocone, and surrounds a central lake across which there is a very narrow bridge or small fold of enamel. Because of the small metaloph and the receded position of the tetartocone, the worn surface of the tooth forms a triangle.

P^4 presents equally strange characters: it is extended transversely but is squeezed in between P^3 and M^1 so that it is longer on the inner side than along the ectoloph. The wide extension inward forms a gentle slope from the deuterocone, but more especially from the tetartocone to the cingulum. The metaloph is relatively larger than that of P^3 and widely separated from the protoloph. On the right tooth, a sharp ridge, on the left a low broad one,

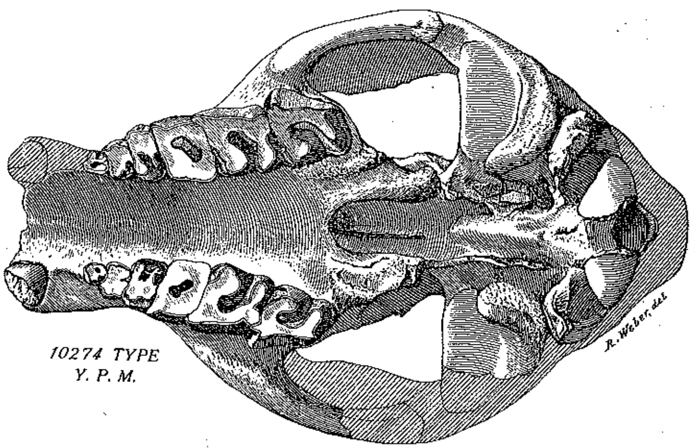

FIG. 2.—*Metamynodon rex*, sp. nov. Holotype. Palatal view of skull showing great reduction of premolars with P^2 rotated, deep posterior nares, heavy canine, and posterior extension of ectoloph on M^3. × 1/6.

unites the two inner cones. There is a sharp crista dividing the internal lake (medisinus), and numerous small folds on the metaloph represent the crochet.

The outer wall of the ectoloph on each premolar shows a heavy central buttress set off by vertical grooves in front and behind; this represents the central protocone, with the tritocone and parastyle behind and in front respectively.

M^1 is so worn that no characters remain except a faint cingulum on the outer side, together with a small

lake or remnant of the diagonal medisinus. The tooth forms a parallelogram elongated transversely; its diameters are 37 and 53 mm.

M^2 has its back, inner, and front sides at right angles, but the outer side is an oblique line. The longest dimensions are, on the outside, 51 mm., and the front side, 60 mm. The medisinus forms a deep sharp groove, directed inward and then forward, uninterrupted by a cingular ridge or basal cusp on its outer end; the postsinus is rather deep, with a sharp fold inward. M^1 and M^2 show no groove, at the present state of wear, separating the parastyle; thus the outer walls are smooth and flat. M^3, however, shows this groove distinctly.

In form, M^3 is very much like M^2, but it has a narrower posterior side; it has the postsinus formed by the extension of the ectoloph, so typical of the family and so different from all other Oligocene rhinoceroses. On this tooth the internal basal cingulum swings into the medisinus, partly filling the groove. The posterior cingulum is much lighter than that of *Amynodon*. In contrast to the premolars, there are no folds of enamel on the walls of the transverse crests, but the enamel of the molars is generally thick and heavy.

A portion of the right ramus No. 12043 of a fossil rhinoceros may belong to a *Metamynodon;* the three teeth are probably P_4, $M_{1\cdot 2}$; they increase rapidly in size so that the M_2 is larger than that of any Oligocene rhinoceros known to the writer. Its great length and high crown are very striking features. The small premolars and the probable lack of P_1, perhaps of P_2, lend weight to the identification as *Metamynodon.*

Summary of Metamynodon rex, sp. nov.—The main differences between the two species of *Metamynodon* may be summed up as follows: premolars of *M. rex*, sp. nov., only submolariform; the type has no postorbital prominence rising from the malar such as appears in *M. planifrons;* the zygomatic suture either forms a sharp angle or leads from within the orbit; P^2 has three fangs instead of two. The much smaller molar length, relative to the premolar length, results partly from the greater age and wear, especially on M^1.

Measurements.

	M. planifrons Scott & Osborn 1887. mm.	*M. rex* Holotype mm.
Skull, length, incisor to condyles	550	520+
Width across arches	365	360
Face, orbit to premaxillary, ant.	170	? 111
Cranium, ant. of orbit to occiput	385	350
Molar-premolar series, length	225	202
Molar series, length	160	140
Premolar series, length	65	61
Diameters of teeth:		
C^1, ant.-post.	35	28.6
C^1, transverse	35	36
P^4, ant.-post.	25	23
P^4, transverse	45	43.4
M^1, ant.-post.	47	36
M^1, transverse	68	56
M^3, ant.-post.	60	58
M^3, transverse	64	60

Amynodon erectus, sp. nov.

(Figs. 3-6, 7*b*.)

Holotype, Cat. No. 11453, Y. P. M. Upper Eocene (Uinta beds), White River, Utah.

The type of this new species is the well preserved skull and jaws used by Professor Marsh in amplifying the description of *A. advenus* (1877, p. 251), figured by him in

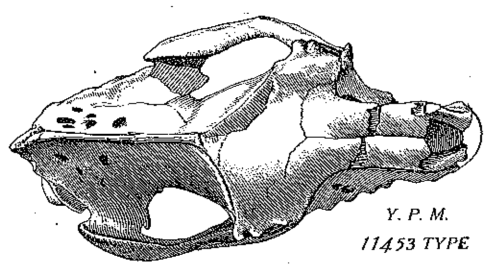

Fig. 3.—*Amynodon erectus*, sp. nov. Holotype. Top of skull showing left side crushed forward. × 1/6.

his work on the Dinocerata and used in the study of brain capacities in extinct mammals (1884, p. 62, fig. 72). The valuable internal cast of the cranium is still available for

comparison and study. The specimen itself has been improved recently by further preparation and now becomes the holotype of a new species.

The genus *Amynodon* is much smaller than *Metamynodon*, and its skull has lighter parts, as shown by the zygomatic arch, the occipital condyles, the proportions of the teeth, etc.

Skull.—The posterior nares extend forward to the second molar, otherwise they resemble those of *Metamynodon* in form, in the depth of the opening, and in the prominence of the pterygoids. The external auditory meatus is open below in this genus, as shown by *A. erectus*, sp. nov.

The basicranial angle (17.5°) is lower than in *Metamynodon* (25°); this is considered a primitive character generally, but here the decrease is partly due to crushing. The premaxillary appears as a narrow strip, barely visible externally; the nasals fold down one third of the distance on the sides; they bear no horn rugosities such as are found in *Colonoceras* (Marsh 1884, p. 62). The deep antorbital depressions are rather broader and more open than in *A. intermedius*, where they are abrupt. There are two suborbital foramina on the right side, through which the nerves and blood-vessels reached the face. The supra-orbital ridge is roughened, and tubercles extend over and in front of the orbits.

Dentition.—There still remain the roots of the second and third upper incisors measuring about 9 mm. in diameter; the median incisor is broken away entirely. The canine alveolus measures 19 by 12 mm. In all probability this tooth was not procumbent as in *A. intermedius*, but was more like that of *A. antiquus* (Scott and Osborn 1883); its shape and position can best be judged by the lower canine, which rises and curves backward almost as in *Archæotherium* and is worn in a similar manner on the posterior side. From the canine to the second premolar there is a diastema of 23 mm.

The total measurement of the premolars, 50 mm., equals half that of the true molars, 98 mm. They are therefore almost as reduced as are those of *A. intermedius*, but that species includes its vestigial P^1, which is absent in the new species. It is seen from the wear on the lower teeth of *A. antiquus* also that P^1 was present. P^4 measures 31 by 19 mm.; the outline is well preserved and the worn enamel indicates a broad shelf on the postero-internal corner. Remnants of the internal lake indicate the presence of the two transverse crests as in other specimens.

M^1 is subquadrate in form and is much shorter, antero-posteriorly, than it is wide (27 by 38 mm.). M^2 forms an irregular quadrilateral with the longest sides anterior (42 mm.) and exterior (43 mm.). The outer side of its ectoloph is apparently entirely smooth, the cingulum and the groove marking off a parastyle both being lost by wear. On M^2 and M^3 there are heavy posterior cingula inclosing depressions (postsinus) and the broad inconspicuous antecrochets are set off by grooves extending down the protocones.

M^3 has three sides at right angles, while the side of the ectoloph runs on a diagonal. The diameters are: antero-posterior, 36 mm., and transverse, 39 mm. The outer side of the tooth is divided into two areas, or grooves, by

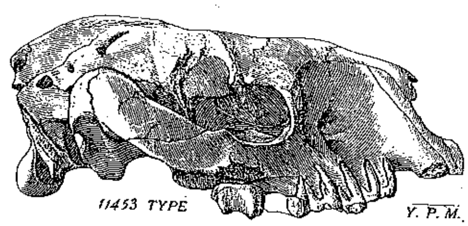

FIG. 4.—*Amynodon erectus*, sp. nov. Holotype. Side view of skull. × 1/6.

a strong ridge opposite the paracone. There is a distinct parastyle. The continuation of the ectoloph beyond its union with the metaloph offers one of the distinguishing features of the Amynodontidæ.

The postsinus is much deeper than that in the holotype of *A. advenus* Marsh (Cat. No. 11763, Y. P. M., fig. 7). In the latter the cingular ridge does not inclose a depression, anterior or posterior, nor does the cingulum extend across the end of the median valley. On the other hand, M^3 of *A. erectus*, sp. nov., in fact, each of the molars, has a strong cingulum anteriorly and a decided internal basal ridge extending across the medisinus which rises into a small cusp, as in certain diceratheres.

Lower jaws.—One ramus of the mandible is almost complete, including its dentition. The body is narrow

and somewhat rounded, as in *Equus;* the horizontal portion is deep and strong, the ascending ramus is wide (cf. *A. antiquus*) and has a thick anterior border with a deep depression exteriorly.

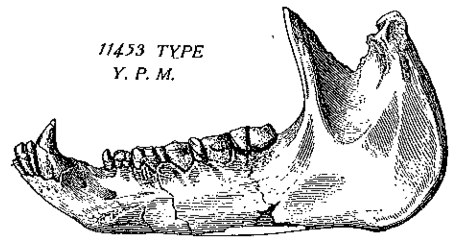

FIG. 5.—*Amynodon erectus,* sp. nov. Holotype. Side view of lower jaws showing erect canines and reduced premolars. × 1/6.

The lower teeth of this new species are of especial interest, furnishing new features of *Amynodon.* The first lower incisor is largest, and is worn off squarely on the end like those of the horse, while the third incisor is smallest and shows the spatulate, subconical crown with a strong cingular ridge on the posterior side. *M. planifrons* is said by Scott and Osborn (1887, p. 167) to reverse this order in the lower jaw, but to follow it in the upper incisors, a rather unusual thing.

The canine leaves the alveolar border directed forward but curves upward to an erect position. It is worn on the front side by the third upper incisor; more significant still, however, is the wear on the posterior side by the superior canine, which must therefore have been much more nearly erect than that of *A. intermedius.* It resembles in this respect *A. antiquus,* which is shown to have had an erect lower canine (Scott and Osborn 1883, pl. 5). The transverse diameter is 16 mm., the antero-posterior 18.5 mm. There is a diastema of about 35 mm. between C_1 and P_2, P_1 being obsolete.

The length of the series of three existing lower premolars is 45.7 mm., of the three molars 97.4 mm. P_2, the first of the series, is small, conical, vestigial; it has two depressions on the inner side, and a basal ridge. P_3 is intermediate in size, but has a form similar to P_4, which in turn is submolariform.

Most of the enamel is broken away from M_1. It is slightly smaller than M_2, which is similar in size and shape to M_3. The last is but little worn and shows well the two crescentic ridges so characteristic of the rhinoceroses.

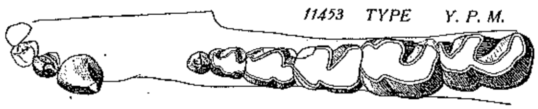

Fig. 6.—*Amynodon erectus*, sp. nov. Holotype. Crown view of lower teeth. × 1/3.

Summary of A. erectus, sp. nov.—The holotype is based on a very well preserved skull and jaws, more primitive than *A. intermedius*, but more advanced than *A. (Orthocynodon) antiquus*. It is smaller than any of the other species. It presents evidence of erect canines both above and below, and in this respect resembles *A. antiquus*; from this species it differs, however, in its later geological age, smaller size, and especially in the absence of both upper and lower first premolars.

The holotype of *A. advenus* Marsh, Cat. No. 11763, Y. P. M., consists of a single third upper molar. *A. erectus*, sp. nov., may be distinguished from it by the stronger cingula both fore and aft, the deeper postsinus, the much narrower medisinus with a basal cingulum and cusp obstructing its opening, and finally, its smaller size.

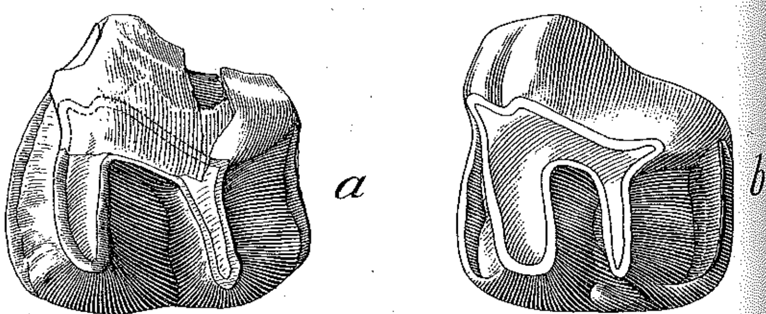

Fig. 7.—*a*, *Amynodon advenus* Marsh. Holotype. Cat. No. 11763, Y. P. M. *b*, *A. erectus*, sp. nov. Holotype. Cat. No. 11453, Y. P. M. Third upper molar of each species. Note the differences of size and form: the variation in the anterior and posterior cingulum, median valley, and internal basal cusp, and the ectoloph extended backward. Nat. size.

Measurements of Holotypes.

	A. erectus sp. nov.	*A. antiquus* (Scott & Osborn) 1883	*A. intermedius* Osborn 1890
	mm.	mm.	mm.
Skull: Length	350		
Length of molar-premolar series	145		187
Length of molar series	96	104	
Diameters of upper teeth:			
P^4, ant.-post.	20	22	
P^4, transverse	32	33	
M^1, ant.-post.	28	37	44
M^1, transverse	39	37	43
M^2, ant.-post.	37	45	53
M^2, transverse	42	37	52
M^3, ant.-post.	36	28	46
M^3, transverse	38	30	46
Lower jaw:			
Length, incisor to angle	356		
Width, body of ramus	45		
Depth of ramus below M_3	74		
Length of premolar series	46	80	
Length of molar-premolar series	142		
Same without M_3	104	165	
Length of molar series	98		
Diameters of lower teeth:			
I_1, transverse	13	9	
I_3, transverse	10		
C_1, ant.-post.	18	15	31
Diastema, C_1 to premolar	34	40	
P_2, ant.-post.	10	19	15
P_3, ant.-post.	15	23	21
P_4, ant.-post.	22	29	26.5
P_4, transverse	16	17	18
M_1, ant.-post.	29	37	35
M_1, transverse	19	24	22
M_2, ant.-post.	34	44	46
M_2, transverse	23		24
M_3, ant.-post.	38		47?
M_3, transverse	20		24

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Art. III.—*New Species of Hyracodon;* by Edward L. Troxell.

[Contributions from the Othniel Charles Marsh Publication Fund, Peabody Museum, Yale University, New Haven, Conn.]

Introduction.

Hyracodon, a genus of rhinoceros-like animals, is known only in the Oligocene. Because of the slender limbs, long neck, and relatively small skull, it was early characterized by Scott and Osborn as cursorial, and it is probable that these light-running ungulates held the place in the economy of nature now filled by the antelope and others of the small ruminants.

Because of the already great reduction of the lateral toes, *Hyracodon* had reached a state of development almost equal to that of *Protohippus,* and, the race persisting, might well have become monodactylous, like the modern horse.

Four species of *Hyracodon* have been made known, only one of which has had figures accompanying the description. Leidy in 1850 gave us the first information of these animals; his later drawings (1852, 1854) have shown a widely diversified group, therefore *H. nebrascensis* in its broadest sense may apply to almost any hyracodont, and the species is virtually synonymous with the genus. The other known species are: *H. arcidens* Cope, *H. major* Scott and Osborn, and ? *H. planiceps* Scott and Osborn.

Discussion of Known Species.

Hyracodon nebrascensis (Leidy).

"A species founded upon a great portion of the face, containing all the superior molar teeth; an inferior maxilla with six molars; and three superior, apparently deciduous molars. It is about the same size as the *R. minutus* of Cuvier.

"Length of line of seven superior molars	4 7/10 inches [119.4 mm.]
Length of line of six inferior molars	4 2/10 inches [106.7 mm.]
Breadth of jaws from the first superior true molar teeth of one side to the other	3 8/10 inches [96.7 mm.]."[1]

It is evident from this and subsequent descriptions that Leidy did not limit himself to one single species, but included specimens with varied features.

Hyracodon arcidens Cope.

The holotype is primarily based on a maxillary with the premolars and M^1 of a very young animal. Cope says:[2]

"The species is about the size of the *H. nebrascensis,* and differs in the form of the inner lobes of the molars and of the first premolar. All the molars have the outer longitudinal and inner transverse crests, the posterior short, the anterior much curved backward round it, and thus forming the inner boundary of the tooth-wall."

This is apparently the first true specific description we have of a hyracodont; it is obviously similar to certain phases of *H. nebrascensis*—it could hardly be otherwise—but applies to that distinctive group, moderate in size, which have the anterior crest much curved backward.

Hyracodon major Scott and Osborn.

The type of this species is a fairly complete skeleton in the Princeton Museum. The species description[3] is based on a fore foot and therefore can not be compared to the new species described later in this paper; unfortunately it does not give any tooth characters and so we know little more than the proportional size of the specimen.

[1] Joseph Leidy, Proc. Acad. Nat. Sci. Phila., 5, 121, 1850.
[2] E. D. Cope, Pal. Bull. No. 15, 2, 1873.
[3] W. B. Scott and H. F. Osborn, Bull. Mus. Comp. Zool., vol. 13, 170, 1887