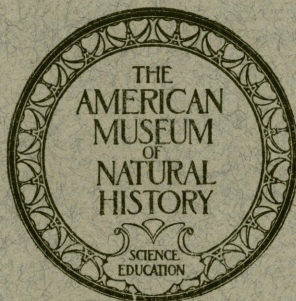


A REVISION OF THE MONGOLIAN TITANOTHERES

BY WALTER GRANGER AND WILLIAM K. GREGORY



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Article X.—A REVISION OF THE MONGOLIAN TITANOTHERES

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INTRODUCTION

The present paper is intended to supplement, revise and complete the earlier reports on the Mongolian titanotheres published by Henry Fairfield Osborn in 1923, 1925 and 1929. At the time of his studies on the group only a part of the material now available had been worked out of the matrix. The entire collection studied by us includes some 141 catalogued specimens, including thirty-seven skulls and seventy lower jaws.

As shown in Osborn's monograph (1929), the earliest known American members of the family (*Lambdotherium*, *Eotitanops*) appeared at the close of the lower Eocene. They were relatively small animals ranging from the size of a whippet hound to that of a sheep. In the succeeding middle and upper Eocene ages their descendants attained a wide diversity of genera and species and ranged in size up to that of a large rhinoceros. In the lower Oligocene some titanotheres surpassed even the larg-

est existing rhinoceroses in size and acquired bizarre specializations in the paired "horns," which consisted of prolongations of the naso-frontal roof, covered with tough skin. Meanwhile the crown patterns of the upper premolars had changed from a condition of relative simplicity, with two or three principal cusps, to stages of increasing complexity in which the crowns of the third and fourth upper premolars finally acquired four main cusps but not a completely molariform pattern. Closely correlated but less conspicuous changes were observed in the lower premolars.

Osborn divided the American titanotheres into many "phyla," or lines of ascent, and in several of them he was able to follow the successive stages of evolution with only small breaks or intervals, at least for part of the entire record. But there were also a number of larger gaps apparently caused by the extinction of particular lines in the known American localities,

¹ Deceased September 6, 1941.

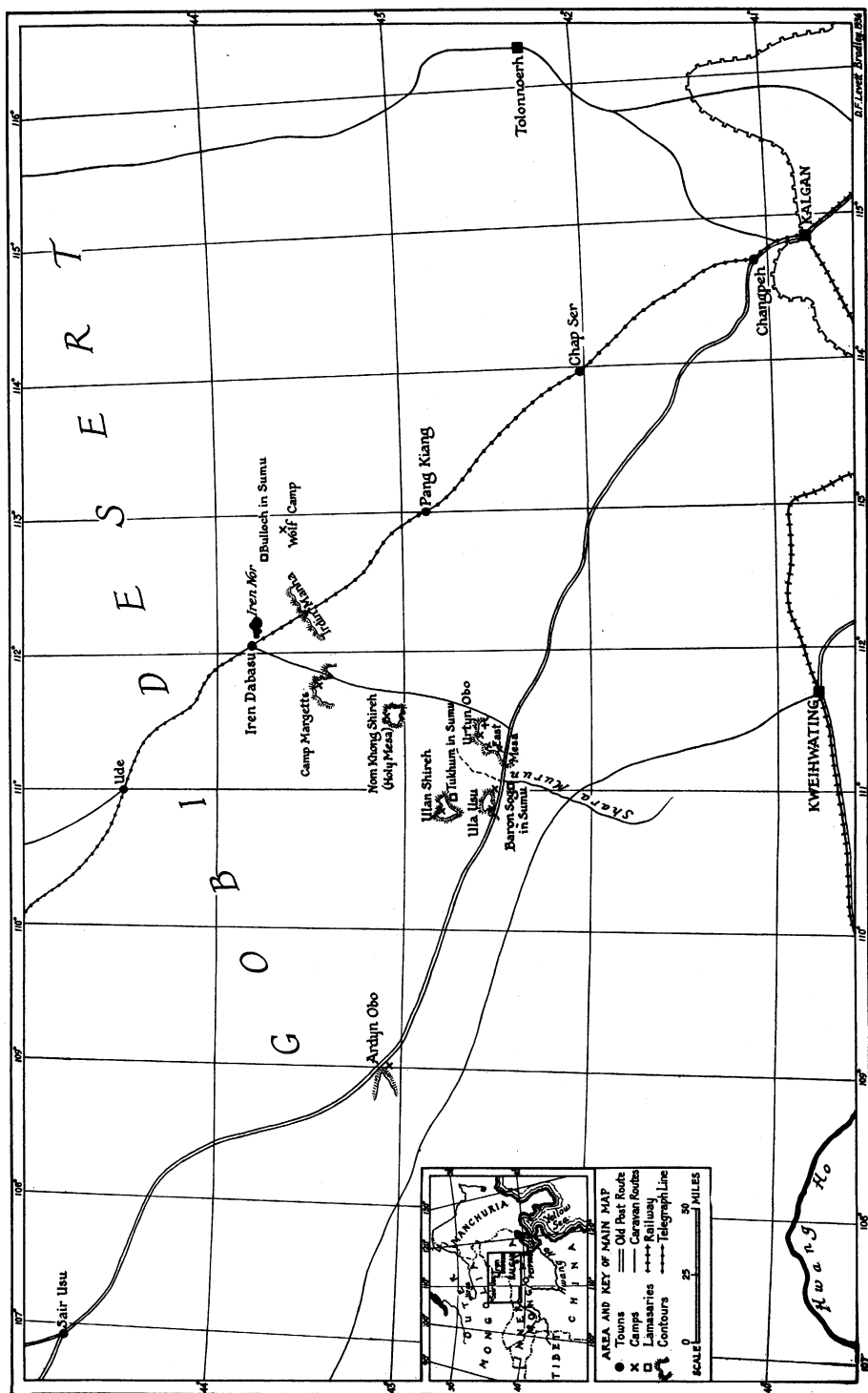


Fig. 1. Sketch map (W. G.) of that part of the route of the Central Asiatic Expeditions showing titanother localities.

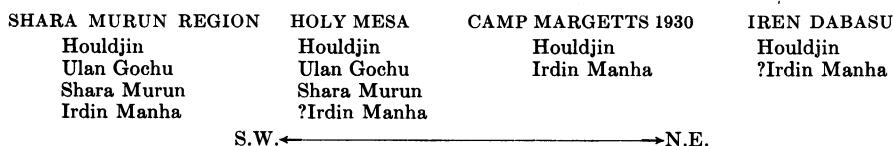


Fig. 2. Correlation of Mongolian formations containing titanotheres. See Fig. 1.

OLIGOCENE	
Houldjin Gravels	<i>Metatitan</i> ,* <i>Embolotherium</i> , <i>Hyotitan</i>
= Baron Sog (type loc.)	
Unconformity	
Ulan Gochu (type loc.)	<i>Embolotherium</i>
? = Ardyn Obo	<i>Parabrontops</i>
	<i>Titanodectes</i>
No unconformity observed	
UPPER EOCENE	
Shara Murun (type loc.)	<i>Rhinotitan kaiseni</i>
	<i>Rhinotitan andrewsi</i>
	<i>Rhinotitan mongoliensis</i>
	<i>Titanodectes</i>
Irdin Manha	<i>Microtitan</i>
= Ulan Shireh (type loc.)†	<i>Epimanteceras</i>
= Tukhum (type loc.)	<i>Gnathotitan</i>
	<i>Desmatotitan</i>
	<i>Metatelmatherium</i>
MIDDLE EOCENE	

Arshanto

* *Metatitan* has been found in the Houldjin Gravels only in the Camp Margetts region, where it is abundant.

† The type locality of Ulan Shireh is some fifteen miles north of Baron Sog Lamasery. The type locality of the Tukhum beds is fifteen miles west of the Lamasery, where they underlie the typical Shara Murun beds. These two localities, together with the Urtyn Obo exposure fifteen miles to the eastward, are all included in the "Shara Murun region."

Fig. 3. Section and faunal sequence in Shara Murun region.

followed by the appearance of other races which had presumably come in to western North America as immigrants from some other center or centers of evolution of the family.

The Mongolian titanotheres, as far as now known, indicate that there was a limited, though at times close connection between the Mongolian and American branches of the family. Apparently some of the descendants of the middle Eocene American species *Telmatherium cultridens* gave rise to the upper Eocene American "*Telmatherium*" *ultimum*, and this in turn

is extremely close to the Mongolian form which we are calling *Metatelmatherium cristatum* and which may therefore be the descendant of American ancestors. The last named species is found in Mongolia in the Irdin Manha formation, which may be of upper Eocene age.

Other Mongolian genera (e.g., *Protitan* and its allies) of Irdin Manha times have every mark of descent from middle or upper Eocene American ancestors: either *Manteceras*, the prophet-horned titanotheres, or the closely related *Telmatherium cultridens*.

In the succeeding Mongolian formation (Shara Murun) the form named *Protitanotherium mongoliensis* by Osborn, although indirectly related to the American upper Eocene genus *Protitanotherium*, appears upon further study to be derived from the earlier Mongolian genus *Protitan*, while Osborn's Mongolian "*Dolichorhinus*" is now seen to differ from its American analogue, the true *Dolichorhinus*, in the very characters in which it agrees with other Mongolian forms. It would appear therefore that the Mongolian titanotheres of the Shara Murun formation were really indigenous to that country, while paralleling their American cousins in certain conspicuous features. Similarly all the later Mongolian forms of the Ulan Gochu and Houldjin formations, even though certain of them were referred by Osborn to the American genera *Brontops* and *Menodus*, now appear in the light of fuller material to be local derivatives of earlier (Shara Murun) Mongolian forms named by us *Rhinotitan*, *Titanodectes*.

On the other hand, so close is the resemblance in the cheek teeth between the Mongolian genera *Parabrontops* and *Metatitan* and the American genera *Brontops* and *Menodus* that it is hazardous to ascribe this all to parallelism, and these American

genera may indeed represent a reflux of immigration from Mongolia, especially in view of the fact that other palaeontological evidence suggests that Mongolia in uppermost Eocene times had faunal connections with both Europe and western North America.

The Mongolian titanotheres are remarkable for their wide diversity in general size. For example, in *Microtitan*, the smallest known Mongolian titanotheres, the adult lower molars (Fig. 5) measure 103.5 mm. in length, while in *Gnathotitan* the corresponding measurement is 235 mm. Secondly, there is an even greater range in the magni-

in such details as might ordinarily be regarded as specific characters. The result is that the number of named "genera" and "species" is large in proportion to the number of known specimens, and it is a safe prediction that future collections from the same region, while broadening still further the diversity of the group, will make it more difficult to separate some of the "species" and "genera" now tentatively recorded as distinct.

In brief, the Mongolian titanotheres are of considerable biological interest because they give us such a clear picture of evolutionary progress and because they illus-

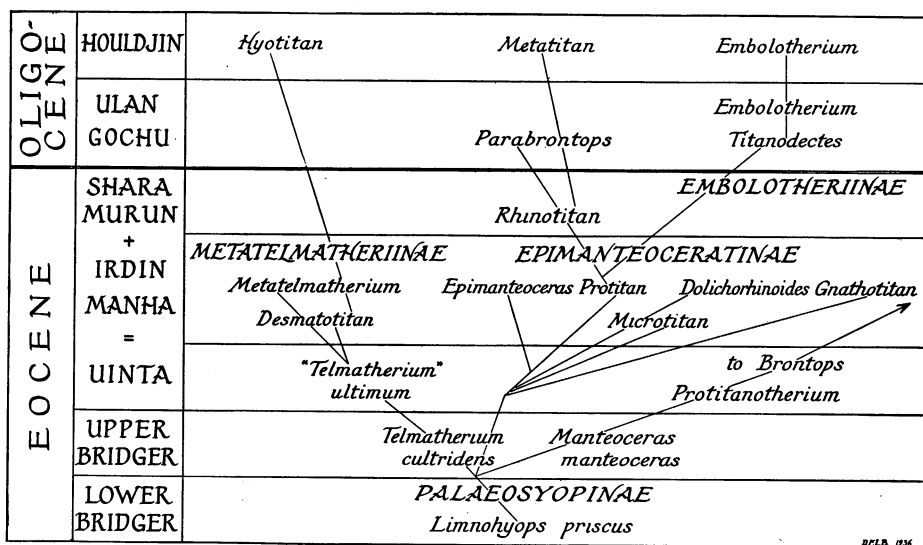


Fig. 4. Provisional phylogeny of the Mongolian titanotheres (W. K. G.).

tude of particular parts: for example, in *Titanodectes ingens* the width of the second lower incisor crown is 27.5 mm.; in the nearly contemporary genus *Parabrontops* the homologous measurement may be as low as 6.5 mm. Even among closely related forms these two factors (differences in general size and differences in the proportional emphasis of particular parts) have produced a baffling array of variations of uncertain taxonomic value, so that in the case of several genera (especially *Protitan*, *Rhinotitan* and *Embolotherium*) among the large number of lower jaws, even in the case of those from the same horizon, hardly any two are exactly alike

trate: (a) retarded evolution in their paired naso-frontal horns; (b) conservatism in the retention of three incisors on each side, both in the upper and lower jaws, together with (c) extremely wide variability both in size as a whole and the relative size and proportions of any given part of the skull and dentition; (d) the effects of long continued isolation in encouraging the production of new and peculiar specializations, as in the genera *Metatitan*, *Titanodectes* and *Embolotherium*; and finally (e), the Mongolian titanotheres, when viewed in the light of what is already known of their relatives in America, indicate that while the earliest known home of the family

was in America in the lower Eocene, certain branches of the family spread to Mongolia just before the upper Eocene and some of their descendants in turn went back to America perhaps before the beginning of Oligocene times. But all branches of the group became extinct before the close of the Oligocene.

For the sake of clearness and convenience our present interpretation of the interrelationships and subfamily classification of the

connections between Mongolia and western North America to make possible the spread of the family from the former to the latter country. Mongolian *Epimanteoceratinae* show a wide range in the characters of the skull and dentition, but the later ones all show an extreme widening of the occiput which is unlike anything found in their American cousins. The naso-frontal horns in this group range from almost nothing in *Dolichorhinoides* to the massive oval swell-

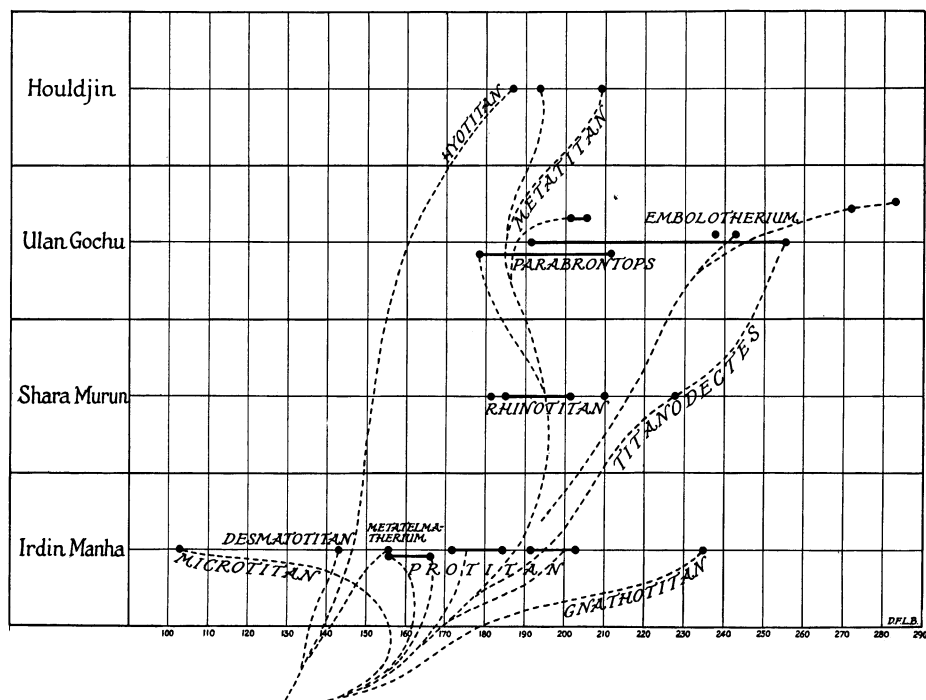


Fig. 5. Progressive increase in length of lower molars in Mongolian titanotheres. Broken lines indicate relationships.

Mongolian titanotheres is summarized in Fig. 4. The diverging lines of Mongolian titanotheres may be grouped under three subfamilies, as defined below. *Metatelmatheriinae*, as far as known, are characterized by their retention of a sagittal crest on the skull, by the lack of naso-frontal horns, by the progressive widening of the lower premolars and shortening of the third lower molars. It is certain that the Mongolian *Metatelmatherium* was closely related to the American *Telmatherium ultimum* and that there must have been some geographic

ings of *Parabrantops*. The incisors in this subfamily range widely from the primitive condition of fairly large size, on the one hand, to extreme reduction (*Parabrantops*), and on the other to marked enlargement (*Rhinotitan*). In *Metatitan*, the last of the entire family, the occiput is extremely broad, but the horns remain very small. The incisors are small.

The third subfamily (*Embolotheriinae*) seems to have been derived either from *Rhinotitan* or from some closely related genus. The nasals grew very large and

were upturned. The opposite horns were connected by a transverse connecting crest and grew far forward, while the free portion of the nasals was eliminated (Fig. 7B, D). Meanwhile the very large permanent incisors failed to come into place and were retained in the alveolar portions of the jaws, at least in some specimens (Fig. 11).

The photographs of skulls here reproduced were made by Mr. Julius Kirschner.

In preparing and assembling the measurements given below we have been ably aided by Mr. G. Miles Conrad, Assistant Curator in the Department of Comparative Anatomy.

Unless otherwise noted, all specimen numbers refer to the catalogue of fossil mammals of The American Museum of Natural History. Measurements are in millimeters.

SYNOPSIS OF MONGOLIAN SUBFAMILIES AND GENERA

- 1.—*METATELMATHERIINAE*: Skull mesaticephalic, zygomata sharply decurved and widely spreading in middle; naso-frontal horn swellings absent or feebly developed; sagittal crest undivided; third upper and lower molars short and broad, p_3 , p_4 relatively wide.

Metatelmatherium: Lower jaw with incurved angular region and not enlarged incisors. Irdin Manha.

Dematotitan: Lower jaw with wide spreading incisors and wide p_3 , p_4 . Irdin Manha.

Hyotitan: Lower jaw with small incisors, very large erect canines, long postcanine diastema, wide, heavily cingulate p_3 , p_4 , short broad m_3 . Ulan Gochu.

- 2.—*EPIMANTEOCERATINAE*: Skull mesaticephalic or dolicho- or brachycephalic, zygomata not so sharply decurved and wide spreading in middle; posterior zygomatic vertical processes usually present. Naso-frontal horn swellings with elongate oval base; sagittal crest divided into paired temporal crests; third lower molars elongate.

Epimanteoceras: Skull mesaticephalic, horn swellings small, nearly above orbits; auditory groove open below; p^3 , p^4 with well developed tetartocones, upper molars but little elongated anteroposteriorly. Irdin Manha.

Protitan: Skull mesaticephalic, horn swellings small, well in front of orbits; auditory groove open below; p^3 , p^4 with little or no tetartocone, upper molars slightly elongate anteroposteriorly; p_2 - p_4 typically compressed. Irdin Manha.

Dolichorhinoides: Skull dolichocephalic, with slight naso-frontal convexities and long nasals; upper molars elongated anteroposteriorly; p^3 , p^4 with tetartocones. Irdin Manha.

Microtitan: Skull unknown; upper molars elongate anteroposteriorly, p^3 , p^4 transversely narrow, without tetartocones; lower premolars markedly compressed, lower molars with

U-shaped proto- and hypoconids Irdin Manha.

Gnathotitan: Skull very dolichocephalic, probably not fundamentally different from that of *Dolichorhinoides*; upper molars excessively elongated anteroposteriorly; upper premolars wide, without tetartocones. Lower jaw enormous, with excessively deep ramus, long, sharply upturned symphysis, relatively large spoon-shaped incisors, and excessively elongated m_3 . Irdin Manha.

Rhinotitan: Skull dolichocephalic, with long, somewhat upturned nasals usually having inrolled lower margins; auditory groove beginning to be closed below; naso-frontal horns small; occiput wide but little if at all produced behind occipital condyles; p^2 - p^4 relatively advanced, with prominent tetartocone ridge or small tetartocones; lower jaw with large incisors and more or less incisor-like canines, forming a spatulate series; p_3 - p_4 relatively large and advanced, m_3 moderately elongate. Shara Murun.

Pachytitan: Closely related to *Rhinotitan* but with stout naso-frontal horn swellings and massive, gently upturned nasals with strongly inrolled lower margins. Shara Murun.

Parabrontops: Skull much as in *Metatitan*, but horns larger; upper premolars advanced, with strong internal cingula, upper molars broad with accessory cristae and crenulate enamel; upper incisors small. Lower jaw stout, with minute nubbins-like incisors. Ulan Gochu.

Metatitan: Skull brachycephalic, with excessively broad, nearly flat occiput; auditory groove closed below by flanges from posttympanic and postglenoid processes; horns small, with transverse connecting region; nasals wide and relatively flat, zygomata expanded slightly at posterior end, postzygomatic vertical processes con-

spicuous; upper and lower molars large, crowding the relatively small premolars, the latter, however, relatively advanced; upper incisors small and nubbin-like, arranged in a flat transverse row; lower incisors small but not minute; lower postcanine diastema crowded out; lower molars not greatly elongated anteroposteriorly. Ulan Gochu, Houldjin.

- 3.—**EMBOLOTHERIINAE:** Skull brachycephalic, with widely expanded zygomata; naso-frontal region upturned and forming an enormous "battering-ram"; auditory groove closed below; second and third upper molars very wide, upper premolars

advanced; lower premolars advanced; third lower molar very large, elongate.

Titanodectes: Very large lower jaw with enormous incisors and relatively small canines; cheek teeth close to those of *Embolotherium*. Shara Murun, Houldjin.

Embolotherium: Upper incisors and canines typically greatly reduced in size (possibly representing retained deciduous teeth), arranged in a spatulate series in the reduced premaxillo-maxillary rostrum; lower incisors and canines the same, likewise with very large successional incisors buried in the jaw. Ulan Gochu, Houldjin.

DESCRIPTIONS OF SUBFAMILIES, GENERA AND SPECIES

Metatelmatheriinae, new subfamily

Skull mesaticcephalic, zygomata sharply decurved and widely spreading in middle; naso-frontal horn swellings absent or feebly developed; sagittal crest undivided; third upper and lower molars short and broad, p_3 , p_4 relatively wide.

METATELMATHERIUM, GRANGER AND GREGORY¹

GENOTYPE.—*Metatelmatherium cristatum*.

REFERRED SPECIES.—*Telmatherium ultimum* Osborn.

GENERIC CHARACTERS.—Skull long, narrow and high; zygomata large, deep, decurved, middle portion widely arching transversely but without buccal swellings, infraorbital portion with prominent longitudinal fossa for insertion of suborbital portion of masseter; supraglenoid processes of zygomata rounded, not acuminate; sagittal crest present, high, undivided, lambdoidal crests thin and prominent, the occiput as a whole being relatively high and narrow; free nasals, short, not upturned, subnasal notch short; naso-frontal horn swellings absent or at most feeble; frontals transversely arched with relatively small and pointed postorbital processes; supra-orbital portion of frontals not forming a projecting shelf above orbits; preorbital surface of maxilla anteroposteriorly short and bearing a large shallow depression in front of the infraorbital foramen; postglen-

noid processes located relatively far back, near the occipital condyles, which are relatively delicate; basioccipital narrow, with high median keel and very prominent tubera basioccipitalia; upper incisors $\frac{3}{3}$, large, heavily cingulate, i^3 almost subcaniniform, with a relatively high, recurved, pointed tip; upper canines large, with high, tapering, recurved crown and sharp anterior and posterior cutting edges, the roots in the male skull being extremely massive; a short postcanine diastema; p^1 relatively large, not compressed, with broad posterior lobe; p^2 , p^3 , p^4 close to those of *M. ultimum*, except that the relative width of p^4 is less, p^3 with low tetartocone ridge, p^4 without recognizable tetartocone; upper molars all relatively wide, much wider than in *Protitan* or *Epimanteoceras*; lower jaw short, deep and relatively thick (in male type), with gently inflected angular region and short space between m_3 and the low coronoid process; lower incisors (at least in male) relatively small, strongly procumbent, arranged in a nearly transverse row; lower canines with very massive roots and recurved, suberect crowns; a prominent postcanine diastema and apparently a short diastema behind p_1 ; p_1 with thick oval crown; lower molars short anteroposteriorly; p_3 with talonid decidedly wider than trigonid; cusps of cheek teeth conic, swollen, cheek teeth with external cingula faint or absent.

REMARKS.—The type skull of *Telmatherium ultimum* Osborn from the Uinta

¹ 1938, Bull. Amer. Mus. Nat. Hist., LXXIV, Oct. 14, p. 435. Addendum to "Fossil Mammals from Burma in The American Museum of Natural History" by E. H. Colbert.

(upper Eocene) of North America so closely resembles the type of our *Metatelmatherium cristatum* in all aspects that one can barely discover specific differences between them, while their congeneric relationship becomes more evident the longer they are studied. Why then are we proposing to erect a new genus *Metatelmatherium* for the reception of these two skulls instead of referring them both to *Telmatherium*? The answer is that, in our opinion, they represent a distinct generic stage characteristic of the upper Eocene of North America and Mongolia, a stage which is much larger and has more advanced premolars than the true *Telmatherium*, which we reserve for the middle Eocene forms *Telmatherium validum* Marsh and *Telmatherium cultridens* Osborn, Scott and Speir.

***Metatelmatherium cristatum*, new species**

Plate II, figures A, B, C; Plate III, figures A, B

HOLOTYPE.—Amer. Mus. No. 26411, a skull and lower jaw.

HORIZON AND LOCALITY.—Irdin Manha, Camp Margetts.

SPECIFIC AND INDIVIDUAL CHARACTERS.—Size larger than that of *M. ultimum*; basal length, 585 ±; transverse zygomata, 330 ±; p^1-m^3 , 233; p^1 very large, roundly compressed; p^2 large, asymmetric; p^3 , p^4 moderately wide with but slight cingulum; anterior border of orbit to front of canine, 190, in *M. ultimum*, 160; occiput relatively broad, height estimated, 190, width at base, 220, index, 86 (in *M. ultimum* the corresponding measurements are 194, 137, 70). Lower jaw differing from that of *M. ultimum* in its short, low, broad, coronoid process, relatively deeper ramus, longer and more sloping symphysis; p_3 relatively wider than in *Epimanteoceras*, relatively less wide than in *Desmatotitan* (see Tables I-IV).

REMARKS.—This species is distinguished from *Protitan grangeri* by the generic characters given above, especially those of the zygomatic arch, occipital crest and broad m^3 . P_3 is notable for its relatively wide talonid, and m_3 is notably shorter than in *E. grangeri*.

***Metatelmatherium parvum*, new species**

Plate III, figures C, D

HOLOTYPE.—Amer. Mus. No. 20168, a fragment of a left lower jaw, with p_3 , p_4 complete and adjacent alveoli of m_1 and p_2 .

HORIZON AND LOCALITY.—Irdin Manha.

SPECIFIC CHARACTERS.—A small Irdin Manha titanotheres with relatively wide talonid on p_3 but with a relatively wide trigonid on p_4 , this combination appearing to ally it with *Metatelmatherium* rather than with *Protitan* (see Table III); external cingulum feeble or absent; premolars much wider than in *Microtitan*, smaller than in *Protitan*, not so wide as in *Desmatotitan*.

REMARKS.—This puzzling specimen appears to be more or less intermediate, as far as it goes, between *Metatelmatherium* and *Desmatotitan*; it also recalls *Protitan*. This fact, together with the excellent preservation of p_3 , p_4 in the type, must be our apology for basing a specific name on such a small fragment.

DESMATOTITAN, NEW GENUS

GENOTYPE.—*Desmatotitan tukhumensis*.

GENERIC CHARACTERS.—Relatively small Metatelmatheriinae, Mongolian Eocene; m_3 remarkably short, with wide talonid and abbreviated hypoconulid; m_2 , m_1 with broad talonids; p_3 with very wide talonid and no metaconid; p_4 wide; external cingulum on p_3 - m_3 strong; incisors and canines relatively large, not unlike those of *Protitan grangeri* and *Telmatherium cultridens*; jaw rather deep in middle but rising gently to the spatulate incisor border; p_1 apparently separated by a considerable diastema from p_2 .

REMARKS.—The name *Desmatotitan* is given in allusion to the more or less annectant characters of this form between *Telmatherium cultridens* and *Metatelmatherium cristatum*. Resemblances and relationships with the type lower jaw of *Metatelmatherium cristatum* are relatively close, but presumably generic differences from *Metatelmatherium*, its nearest ally, are the much smaller and more slender jaw, the relatively large spreading incisors, the relatively larger p_3 , p_4 , and very wide talonid on p_3 , the shorter and wider m_3 and the heavy external cingulum on p_3 - m_3 .

The type jaw and teeth are much too small to fit the type skull of *Epimanteoceras formosus*, although the wide premolars are rather suggestive of that form. This genus, although probably derived from *Telmatherium cultridens*, is much more advanced in the evolutionary stages of its premolars and in the relative width of m_3 . The present genus differs most widely from *Gnathotitan* in its relatively short and wide m_3 and in the wide talonids on p_2 - p_4 .

Desmatotitan tukhumensis, new species

Plate III, figures E, F

HOLOTYPE.—Amer. Mus. No. 21606, a lower jaw, including the right ramus and entire symphysis.

HORIZON AND LOCALITY.—Ulan Shireh (= Ir-din Manha) formation, four miles north of Tukhum Lamasery, Mongolia.

SPECIFIC CHARACTERS.—In the absence of other jaws of the same genus it is difficult to distinguish between specific and generic characters (Tables III, IV).

HYOTITAN, NEW GENUS

GENOTYPE.—*Hyotitan thomsoni*.¹

GENERIC CHARACTERS.—Large persistent metatelmatherines of relatively late (Houldjin) age; lower jaw with extremely large upcurved lower canines, a long postcanine diastema and narrow channel for the tongue, relatively short and wide cheek teeth and small lower incisors; symphysis long, sloping; front of jaw and ramus (corpus) but little swollen; m_3 with external cingulum.

REMARKS.—This genus may well be a successor of *Desmatotitan*, which it resembles in general, especially in the shortness and width of its cheek teeth. It is apparently excluded from close relations with *Protitan* and *Epimanteoceras* by the great relative width of the premolars and molars. A similar combination of characters (incisors $\frac{3}{3}$, small, a long postcanine diastema, advanced premolars and wide molars) is found in the American species *Eotitanotherium osborni* Peterson from the uppermost Eocene.

Hyotitan thomsoni,¹ new species

Plate IV, figures A, B

HOLOTYPE.—Amer. Mus. No. 26401, a lower jaw.

HORIZON AND LOCALITY.—Camp Margetts, Houldjin level.

SPECIFIC CHARACTERS.—Size much larger than in *Desmatotitan tukhumensis*, p_1-m_3 , mid-length, 309, m_1-m_3 , 187. (See Table III.) Incisors much smaller than those of *Desmatotitan*.

REMARKS.—Although this is one of the latest of the titanotheres, it is relatively primitive, that is, much more like the jaws of Ir-din Manha representatives of *Protitan grangeri* than are the jaws of its highly

specialized contemporaries, *Metatitan* and *Embolotherium*.

Epimanteoceratinae, new subfamily

Skull mesati- to dolicho- or brachycephalic, zygomata not sharply decurved or widely spreading in middle, posterior zygomatic vertical processes usually present. Naso-frontal horn swellings small or moderate in size with elongate oval base; sagittal crest divided into paired temporal crests; third lower molars more or less elongate.

REMARKS.—A careful reconsideration of the evidence leads us to the conclusion already put forward by one of us,² that the subfamily Manteoceratinae was much more closely related in its basal forms to the Telmatheriinae than was admitted by Osborn.³ Unquestionably certain specimens (Amer. Mus. Nos. 12193, 12194) from the Bridger basin in Wyoming are intermediate in character between *Telmatherium cultridens* and *Manteoceras manteoceras*, while certain Mongolian forms, especially *Protitan grangeri* and *Epimanteoceras formosus*, show in their upper and lower teeth most unmistakable evidence of this double relationship.

EPIMANTEOCERAS, NEW GENUS

GENOTYPE.—*Epimanteoceras formosus*.

GENERIC CHARACTERS.—Mongolian upper Eocene Epimanteoceratinae of moderate size with small naso-frontal horns almost directly above the eyes, more advanced than in *Manteoceras* but less so than in *Protitan* and *Protitanotherium*. Nasals long, with inrolled lower borders, slightly expanded, transversely truncate tip. Postorbital processes very large, frontal region broad, flat. Opposite temporal crests well separated. Occipital crests extending well behind condyles. P^2 , p^3 , p^4 relatively short and wide, p^3 , p^4 with well developed tetartocones. M^3 but little elongate anteroposteriorly. Canines (σ) very stout.

Epimanteoceras formosus, new species

Plate V, figures A, B, C

HOLOTYPE.—A nearly perfect skull, Amer. Mus. No. 21613, lacking only the lower jaw.

HORIZON AND LOCALITY.—Ulan Shireh (= Ir-din Manha), four miles north of Tukhum Lamasery, Mongolia.

¹ Named in honor of Mr. Albert Thomson, formerly chief preparator of the Department of Palaeontology, The American Museum of Natural History, and member of the Central Asiatic Expeditions of 1928 and 1930.

² Gregory, W. K., in Osborn, H. F., The Titanotheres of Ancient Wyoming, Dakota and Nebraska, 1929, U. S. Geol. Surv., Monogr. 55, I, p. 339, footnote.

³ *Op. cit.*, p. 339.

SPECIFIC CHARACTERS.—Upper incisors un-reduced, canine roots extremely massive; over-all tooth measurements not far from those of *Protitan grangeri*, but m^3 less elongate, m^2 wider than long, p^4 relatively much wider than in *P. grangeri* type; m^1 - m^3 , 157; postcanine diastema short (23 +); no paired pits on inferior surface of basisphenoid, postzygomatic "horns" wanting; postglenoid located far forward. P_1 with simple compressed crown, anterior root large and inclined forward; p^2 wide, somewhat asymmetric, with very large deuterocone; p^3 wide, subquadrate, with good-sized tetartocone in worn state; p^4 wide with large tear-shaped tetartocone; m^1 small, squarish, m^2 slightly elongate, m^3 relatively normal with small hypocone loph separated from cingulum; secondary postnarial rim short; no basisphenoid pits; zygomatica deep in middle; postorbital processes large, conspicuous; horn swelling small, directed chiefly outward. Lower jaw not known. The distance from the anterior edge of p^2 to the hypocone fossa of m^3 (about 225 mm.) should be equal to the distance from the tip of the hypoconulid of m^3 to the tip of p^2 . None of the available lower jaws from the Irdin Manha will fit on this skull exactly (Tables V, VII).

REMARKS.—This is one of the best preserved of all known titanotheres skulls. It is distinctly advanced beyond the stage of *Manteoceras* and in the direction of *Rhinotitan*. It is readily distinguished from the skull of *Protitan grangeri* by the small size of the horn swellings, which are almost directly above the anterior border of the orbits instead of widely in front of them. The upper premolars are unusually wide and progressive.

A careful series of measurements of the known dimensions of the upper teeth of *E. formosus* indicates what the measurements between the corresponding parts of the lower teeth should be, as follows:

	<i>E. formosus</i>	<i>P. minor</i> ref. (Amer. Mus. No. 26410)
Inc. alv. to cond. should be	558 mm.	440
P_1 - m^3 should be	250	240
M_1 - m^3 " "	163	162
P_1 - p^4 " "	86	90
P_2 - p^4 " "	73	78
M_3 " "	66	72
M_2 " "	56	48
M_1 " "	40	38
P_4 " "	24	24
P_3 " "	19	22
P_2 " "	25	21

Unfortunately no known lower jaw fulfills these requirements exactly, and this

circumstance tends to emphasize the distinctness of *Epimanteoceras* from allied genera. However, *Epimanteoceras* is distinguished by the relatively great widths of p^3 , p^4 , and the somewhat corresponding widths of p_3 , p_4 are to be found in Amer. Mus. No. 20104, the type of *Protitan robustus*. This jaw also suggests *Epimanteoceras formosus* in its large, robust, erect canines, in its large lower incisors and well marked postcanine diastema. The very distinct tetartocones on p^3 , p^4 imply the presence of equally prominent entoconid ridges on p_3 , p_4 . This character is absent in jaws referred to *Protitan grangeri*, *P. minor* and *P. robustus* but is well indicated in jaws Amer. Mus. Nos. 26410, 26408 and 26415 from Camp Margetts, Irdin Manha formation. Nevertheless no one of these jaws will fit the type skull of *Epimanteoceras formosus*, and we have referred them on other grounds also to different species.

PROTITAN, NEW GENUS

GENOTYPE.—*Protitanotherium grangeri* Osborn.

GENERIC CHARACTERS.—Mongolian epimanteoceratines, Irdin Manha formation; skull mesaticephalic, with broad flat forehead; nasofrontal "horns" oval, well in front of the eyes and far anterior to the postorbital process; nasals rounded distally and somewhat decurved, not tubular; zygomatica with prominent posterior vertical processes; m^3 moderately elongate anteroposteriorly; p^3 , p^4 with small or no tetartocones. Basioccipital with low median keel; lower incisors of relatively large size, arranged in a spatulate row, lower postcanine diameter long; p_1 very small, simple; p_2 compressed; p_3 without marked expansion across the talonid.

REFERRED SPECIES.—*Protitan robustus*, *P. minor*, *P. bellus*.

REMARKS.—The type of *P. grangeri* differs from the type of *Protitanotherium emarginatum* especially in the lower jaw (see table at top of next page).

The nasals of the type of *P. grangeri* are more tapering, less truncate than those of the type of *P. emarginatum*; its "horns" are smaller and less elevated, upper incisor teeth less reduced and less transverse in position; upper canines much smaller (but this may be due to a difference in sex).

These differences collectively indicate a generic difference from the American

	<i>Protitan grangeri</i>	<i>Protitanotherium emarginatum</i>
Geological horizon	Irdin Manha	Uinta
Lower incisors	Of relatively large size, arranged in a spatulate row	Much smaller, more transverse
Lower postcanine diastema	Long	Short
P ₁	Very small, simple	Large, more complex
P ₃	Relatively shorter	Relatively longer
General size	Smaller	Larger
Symphysis	Massive	More slender

Protitanotherium, the latter appearing to be on the whole more advanced in the direction of the smaller species of *Brontops*.

Protitan grangeri (Osborn)

Plate IV, figures C, D; Plate VI, figures A, B; Plate VII

Protitanotherium grangeri OSBORN, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, p. 7.

Dolichorhinus olseni OSBORN, *ibid.*, p. 10.

Manteoceras? irдинensis OSBORN, *ibid.*, p. 11.

HOLOTYPE.—A well preserved skull and lower jaw, Amer. Mus. No. 20103.

HORIZON AND LOCALITY.—Irdin Manha formation, one-half mile south of the Kalgan-Urga telegraph line.

REFERRED SPECIMENS.—Various specimens from the Irdin Manha formation, especially the following: Amer. Mus. No. 20114, front of skull, including nasal bones; Amer. Mus. No. 20120, m¹-m³, right; Amer. Mus. No. 20108, a right maxilla; Amer. Mus. No. 20013, front of skull with nasals; Amer. Mus. No. 26408, a lower jaw; Amer. Mus. No. 20109, a lower jaw, the type of *Dolichorhinus olseni* Osborn; Amer. Mus. No. 20111, front part of lower jaw, with incomplete symphyseal region, the type of *Manteoceras? irдинensis* Osborn.

SPECIFIC CHARACTERS.—The measurements in Table V show that in the type of *P. grangeri*, as compared with the other species of the genus, the skull is relatively wider across the zygomata, the third upper molar is of intermediate breadth, the first upper molar moderately narrow, p⁴ not very wide. In the lower jaw the incisors are large and spreading, p₂, p₃ compressed, p₃ with metaconid, p₄ not wide and with little or no external cingulum (Table VI).

REMARKS.—In the lower jaw of the type of *P. grangeri* the symphysis is crushed down, decreasing its true height and lengthening the over-all measurement (Table VI, incis. alv. to cond.) as well as the postcanine

diastema. Otherwise its dimensions agree with those of *P. olseni*, except in m₃ which is somewhat shorter. On the whole, therefore, *P. olseni* (Amer. Mus. No. 20109) may be regarded as synonymous with *P. grangeri*.

The type jaw of *Manteoceras? irдинensis* Osborn (Amer. Mus. No. 20111) is generically referable to *Protitan*. The alleged shallowness of the symphysis is due to the lack of its upper front part. In the dimensions of its molars this jaw somewhat exceeds those of *P. grangeri* but does not equal those of *P. robustus*. The type is a poor fragment and may be regarded as synonymous with *P. grangeri* which has "page priority" in the original description (Table VI).

Protitan minor, new species

Plate VIII, figures A, B, C

HOLOTYPE.—Amer. Mus. No. 26416, a skull, lacking the distal end of the nasals.

HORIZON AND LOCALITY.—"Probably top of Irdin Manha beds," Camp Margetts, 1930.

REFERRED SPECIMENS.—Amer. Mus. No. 26417, front part of skull, with teeth, Camp Margetts; lower jaws: Amer. Mus. Nos. 26410, 26413, 26415, 26418, from same locality.

GENERIC CHARACTERS.—Horns intermediate in stage between *Manteoceras* and *Protitanotherium*. Upper incisors the same. Postzygomatic "horns" well developed. Auditory groove widely open.

SPECIFIC CHARACTERS.—P¹ small, compressed; p² oblique, asymmetric, narrow; p³ narrow; p⁴ not nearly so wide as in *E. formosus*; m¹ of moderate width, m² narrow, m³ fairly narrow; p⁴ with slight tetartocone ridge but no cusp. Zygomata not wide. Basisphenoid pits conspicuous. Lower jaw not definitely known but the distance from the hypocone to the anterior rim of p² (217), which should be equal to the distance from the hypoconulid to the tip of p₂, is nearly matched in a lower jaw, Amer. Mus. No. 26410, from the same locality and horizon. This jaw agrees well in other measurements and dental characters with the type skull and is therefore referred to this species. It differs from the type of *D. olseni* chiefly in its smaller di-

mensions but tends to confirm the reference of that form to *Protitan grangeri*. Amer. Mus. No. 20108, a maxilla, is close to *P. minor* in general, but the m^3 is much longer. The latter is in an early stage in lengthening, a process which was carried to an extreme in *Gnathotitan* (Tables V, VI).

***Protitan robustus*, new species**

Plate IX, figures A, B

HOLOTYPE.—Amer. Mus. No. 20104, a lower jaw with well preserved dentition.

HORIZON AND LOCALITY.—Irdin Manha formation, Irdin Manha.

DOUBTFULLY REFERRED SPECIMENS.—Amer. Mus. Nos. 20112, right lower jaw, Irdin Manha; 19179, a lower jaw fragment with relatively wide premolars; 26412, a lower jaw; 26409, right lower jaw, p_4-m_3 .

SPECIFIC CHARACTERS.—Size large; incisors large, wide spreading, much like those of *P. grangeri* but wider; canines very massive with recurved crowns; postcanine diastema short (Table VI).

REMARKS.—The teeth, especially the incisors, canines and premolars are much too large and progressive to go with the type of *P. grangeri* or even to be referred to *Epi-manteoceras formosus*. The jaw in its overall measurements would nearly fit the type skull of *Protitan bellus*, but, as shown by detailed measurements, the cheek teeth are for the most part too large to do so.

Amer. Mus. No. 20110, a large lower jaw from the Irdin Manha (Pl. IX, figs. C, D) is of approximately the same size as the type of the present species, but its incisors are much smaller, its canines relatively slender and subvertical, the diameters across the opposite tooth rows remarkably narrow, and its p_3 , p_4 distinctly narrow. This jaw has the teeth somewhat too large to fit with the skull of *P. bellus*. Its coronoid process is nearly vertical, not recurved. In the stage of its p_2-p_4 , as well as in dimensions, it affords an important structural link between *Protitan* and *Rhinotitan* and might well be referred to the latter except that it is much older. The specific reference of this jaw to *P. robustus* is doubtful, but since it comes from the same horizon, we refer it provisionally to that species (Table III).

This jaw is also interesting because in some respects it recalls the type of the American *Protitanotherium emarginatum*. It differs from the latter, however, as fol-

lows: (1) its m_1 is wider; (2) its p_4 much longer and more advanced; (3) its p_3 much wider; (4) its p_2 much larger and more advanced; (5) its p_1 much smaller and more primitive; (6) its canines more slender and erect; (7) its incisors less reduced, with very large posterior cingulum and sharp anterior cingulum.

It also resembles somewhat the type of the American upper Eocene *Telmatherium altidens* Osborn but differs especially in its larger, more advanced p_2-p_4 , smaller p_1 and smaller incisors.

The same jaw in comparison with the type jaw of the American *Protitanotherium superbum* Osborn differs very widely in its smaller general size, its narrowness across the symphysis and in the far more slender form of the canines; its p_2 , p_3 , p_4 are all larger and more progressive, its molars smaller.

These facts suggest that the Mongolian species of *Protitan* differs generically from the American *Protitanotherium*, which may, however, be a fairly near relative, as recognized by Osborn.

***Protitan bellus*, new species**

Plate x, figure A

HOLOTYPE.—Amer. Mus. No. 26104, a beautifully preserved palatal side of a skull with complete dentition and basis cranii.

HORIZON AND LOCALITY.—Irdin Manha formation, Ulan Shireh beds, Spring Camp, East Mesa, Shara Murun region.

SPECIFIC CHARACTERS.—Upper molars anteroposteriorly longer than in *P. grangeri*, especially m^1 ; p^3 with incipient tetartocone swelling, p^4 more elongate; incisors much larger than in the type of *P. grangeri*, outside width across opposite m^3 distinctly larger (Tables V).

REMARKS.—A special series of detailed measurements indicates that the lower jaw which is the type of *Protitanotherium olseni* Osborn has almost the right over-all measurements to fit on this skull; but the anteroposterior measurements of its p_1-m_3 , p_2-p_4 , m_2 are all too small; also the compressed form and delayed evolution of p_2 , p_3 do not accord well with the vigorous development of the corresponding upper teeth. Moreover, the weak incisors and canines of the type of *olseni* contrast widely with the strong incisors and canines of *bellus*; although this may possibly be a sex

difference, it adds to the uncertainty of referring both to the same species. The dimensions of the upper teeth are too small to fit the type lower jaw of *Protitan robustus*.

Protitan obliquidens, new species

Plate x, figure B

HOLOTYPE.—Amer. Mus. No. 20125, part of left maxilla containing p^1 , p^2 , p^3 .

HORIZON AND LOCALITY.—Irdin Manha formation, Irdin Manha.

SPECIFIC CHARACTERS.—Crown pattern of p^2 , p^3 very oblique both on the anterointernal and posterolateral borders, internal oblique ridge on p^2 pronounced, culminating in a low internal cusp; no trace of a separate tetartocone on either p^2 or p^3 . Ectoloph very oblique with high and bulging primary cusp much larger in outer view than the inwardly displaced posterolateral cusp. Internal cingula distinct on p^2 , p^3 with delicately beaded edge. P^1 not differing much from that of *P. grangeri*, *P. bellus*.

REMARKS.—This fragment differs widely from *P. minor* in the markedly oblique form of p^2 , p^3 ; it is close to *bellus* in most fea-

GENERIC AND SPECIFIC CHARACTERS.—Size much smaller than any known species of *Rhinotitan*, smaller than the larger forms of *Protitan* but slightly larger than the typical *P. minor*; much more progressive than any of these forms in the heavy external cingulum on p_2 - m_3 and in the relative width and crowding of p_2 - p_3 . Differing from *Desmatotitan* and *Metatelmatherium* in the much more elongate m_3 . General form of jaw much more primitive than that of *Rhinotitan* and *Metatitan* and not very different from *Protitan* (Table XI).

REMARKS.—This very difficult specimen, doubtfully recorded from the Houldjin, is remarkably advanced in the stage of its premolars, while remaining of relatively small size and retaining a primitive form of the jaw. In dimensions it is most nearly approached by Amer. Mus. No. 26410, a lower jaw which was also doubtfully recorded from the Houldjin but which lacks the external cingula and is in general more or less intermediate between *P. minor* and *P. grangeri*. Notwithstanding its much

COMPARATIVE MEASUREMENTS

	<i>Protitan obliquidens</i>	<i>Protitan bellus</i>	<i>Rhinotitan mongoliensis</i>
P^1 ap. \times tr.	18 \times 11	17 \times 11	20 \times 15.5
P^2 ectoloph (oblique)	28.0	28	29.0
P^2 mid-ectoloph to protocone	25.0	23	29.2
P^2 max. obl. meas. pas. to post. internal cing.	33.0	29	33.5
P^3 ectoloph (oblique)	30.0	29	34.0
P^3 mid-ectoloph to protocone	29.2	28	35.5
P^3 max. obl. meas. pas. to post. internal cing.	38.0	39	41.0

tures except in the much greater maximum oblique width of p^2 . It is far more primitive than *Rhinotitan mongoliensis* in the lack of filling in of the inner side of p^2 , p^3 but may well be ancestral to that form. It differs from *Dolichorhinoides angustidens* in the marked obliquity of the crown, total lack of tetartocone, feeble development of the external ribs of both the paracone and metacone and of the external cingulum. It nearly fits some of the larger jaws of *Protitan* but is too small for Amer. Mus. No. 20112, which we refer to *P. robustus*. In its well marked tritocone-tetartocone ridge this form distinctly foreshadows *Rhinotitan*.

Protitan? cingulatus, new species

Plate ix, figure E; Plate x, figure C

HOLOTYPE.—Amer. Mus. No. 26412, a right lower jaw with p_1 - m_3 complete.

HORIZON AND LOCALITY.—The horizon is doubtfully entered as ?Houldjin. Ten miles west of Camp Margetts.

smaller size, this jaw seems after many comparisons to represent a relatively primitive survivor of *Protitan* but related also to *Metatitan*.

MICROTITAN, NEW GENUS

GENOTYPE.—*Metarhinus mongoliensis* Osborn.

GENERIC CHARACTERS.—The smallest of all known Mongolian titanotheres, about the size of the American *Metarhinus fluviatilis* but differing as follows: p_2 , p_3 , p_4 relatively compressed, with wider talonids, p_4 with lower entoconid; m_3 with larger, more conical hypoconulid and more U-shaped proto- and hypoconids; upper premolars p^2 , p^3 narrower transversely with oblique anterointernal border, cusps more delicate, ectolophs flatter, external cingula less robust. Somewhat resembling the American *Mesatirhinus* and *Dolichorhinus* but with premolars and molars relatively narrower, premolar ectolophs flatter, p^3 , p^4 with fuller inner lobes, p^2 more advanced toward p^3 ; m^3 , m^2 with more prominent mesostyles, m^3 with well formed cuspidate hypocone. Distinctly recalls the American *Telmatherium cultridens* in a general way, especially in the lower cheek teeth

but is distinguished by elongate molars and more advanced premolars both in upper and lower jaws.

After prolonged comparisons *Microtitan* in both upper and lower teeth is seen to be closely related to *Protitan minor*. Still later comparisons show it also to be structurally intermediate between *P. minor*, *Dolichorhinoides* and *Gnaihotitan*. Differs from *Desmatotitan* in its far smaller size, compressed p_2 - p_4 ; external cingula absent on p_2 , p_3 , feeble on p_4 - m_2 . From the several species of *Protitan* it differs in its diminutive size and compressed, sharp cusped lower premolars and U-shaped proto- and hypoconids of m_2 , m_3 . From *Epimanteoceras formosus* it differs in the transverse narrowness of all the

HORIZON AND LOCALITY.—Irdin Manha formation, Irdin Manha.

NEOTYPE.—Amer. Mus. No. 22099, a right p_2 - m_3 complete, with alveolus of p_1 set in incomplete right ramus; from the Ulan Shireh (Irdin Manha) beds, four miles north of Tukhum Lamasery (Table VIII).

REFERRED SPECIMEN.—Amer. Mus. No. 21611, right maxilla with p^2 - m^3 beautifully preserved, from the Ulan Shireh (Irdin Manha) beds, eight miles north of Tukhum Lamasery (Table VII).

SPECIFIC CHARACTERS.—The maxilla ap-

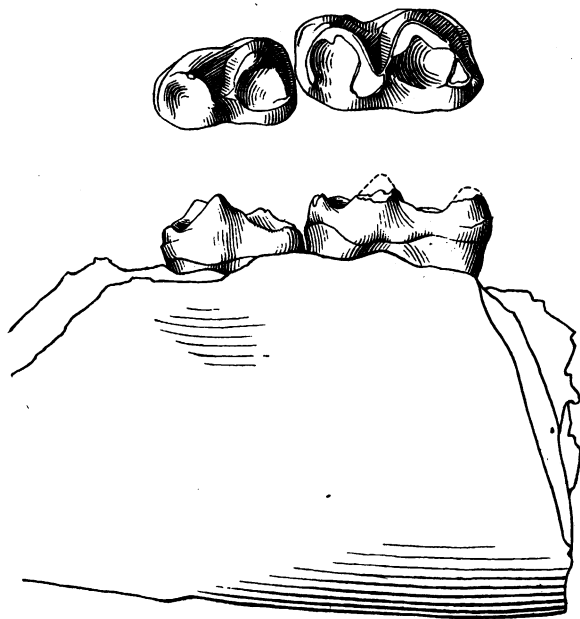


Fig. 6. *Microtitan mongoliensis* (Osborn), type jaw (fragment) of *Metarhinus? mongoliensis*, Osborn Amer. Mus. No. 20167, natural size.

upper cheek teeth, especially the molars, and in the high pointed hypocone on m^3 . The transverse narrowness of the upper molars suggests special relations with *Rhinotitan*, but the upper premolars are more primitive in lacking tetartocone ridges.

Microtitan mongoliensis (Osborn)

Plate XI, figures A, B, C; Figure 6

Metarhinus? mongoliensis OSBORN, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, pp. 11, 12.

HOLOTYPE.—Amer. Mus. No. 20167, a fragment of a lower jaw containing p_4 , m_1 ; a deciduous upper molar (dp^4) may be associated (Table VIII).

proaches that of *E. formosus* (except in its extremely small size), but the infraorbital fossa is further forward, and the nasal notch was probably relatively shorter. P^1 - m^3 measures only 145 mm., as against 249 in *E. formosus*. Approaches *P. minor* in the general stage of its upper premolars, but p^3 is relatively narrow, p^4 has a flatter ectoloph and higher and more pointed cusps, while m^3 has a good hypocone (absent in *P. minor*). The upper premolars have advanced beyond those of the Bridger *Manteoceras*, and the molars are more elongated anteroposteriorly. It differs from *Metarhinus fluviatilis* in its narrower pre-

molars and molars, flatter ectolophs on p^3 , p^4 . The lower premolars are more compressed than those of *Metarhinus fluviatilis*, and the hypoconulid of m_3 is larger and extends farther posteriorly.

REMARKS.—The holotype, while very incomplete, bears p_4 and m_1 which so closely approach those of Amer. Mus. No. 22099 as to leave no reasonable doubt of specific identity. This association establishes differences from *Metarhinus fluviatilis* which appear to be of generic value (see above). The referred upper teeth nearly agree with the lower teeth in size and afford additional distinctions from *Metarhinus*.

Apparently the Mongolian *Microtitan* was a pygmy relative of its compatriot *Dolichorhinoides* in much the same way as the American *Metarhinus* was a pygmy relative of *Dolichorhinus*.

In addition to the compression of the lower premolars, the neotype is peculiar in the U-shaped outer walls of the proto- and hypoconids of the molars, especially m_3 .

DOLICHORHINOIDES, NEW GENUS

GENOTYPE.—*D. angustidens*.

GENERIC CHARACTERS.—Clearly distinguished from the type of *Epimanteceras formosus* (a skull of about the same length) by the extraordinarily narrow, anteroposteriorly elongate molars; also from "*Dolichorhinus kaiseni*" Osborn by the same narrowness of the molars, which are also much narrower than those of *Rhinotitan mongoliensis* and *R. andrewsi*. Naso-frontal horn swellings practically absent, represented only by a low convexity. P^2 , p^3 with large tetartocones; tetartocones not on narrow ridge (contrast *R. mongoliensis*, *R. andrewsi*); p^4 without tetartocone (contrast *mongoliensis*, *andrewsi*). Internal cingulum pronounced, with conspicuous beading. Nasals very long.

REMARKS.—This skull differs conspicuously from those of the American *Dolichorhinus*; it lacks infraorbital tuberosities, its orbits are larger, the postorbital processes of the frontals are less pointed; the anteroposterior curvature of the parietal region of the cranium is wanting, and there is only a low naso-frontal convexity. In some respects *Dolichorhinoides* seems to lead to *Gnathotitan*, especially in the anteroposterior elongation of the molars.

Dolichorhinoides angustidens, new species

Plate XII, figures A, B; Plate XIII, figures A, B

HOLOTYPE.—Amer. Mus. No. 21607, a skull, lacking the occipital region but with well preserved cheek teeth.

HORIZON AND LOCALITY.—Ulan Shireh (= Irdin Manha) formation, eight miles north of Tukhum-in-Sumu.

SPECIFIC CHARACTERS.—Not yet distinguished from generic characters. For measurements, see Table X.

GNATHOTITAN, NEW GENUS

GENOTYPE.—*Telmatherium berkeyi* Osborn

GENERIC CHARACTERS.—Mongolian Eocene titanotheres of gigantic size, with excessively deep lower jaw, very steep symphysis, very large thick spoon-shaped lower incisors; p_1 unusually large, with simple compressed crown and pointed tip, p_2 with simple compressed tip and low, well formed talonid. Postcanine diastemata in upper and lower jaws, moderate to long. Molars elongate anteroposteriorly, m^3 and m_3 excessively so; p^2 , p^3 , p^4 widened transversely. Maxillae elongate, nasal notch long and probably low. Horns unknown; if present probably oval.

REMARKS.—After repeated intensive and extensive study and comparison of available material, we cannot follow Osborn in referring this species to the genus *Telmatherium*. It differs widely from "*Telmatherium*" *ultimum* in so many characters in which it agrees with other Mongolian titanotheres that we cannot believe it has an altogether separate origin from the latter.

It differs from *T. ultimum* in having a far more elongate face and cheek teeth; the infraorbital canal opens much farther forward, and the suborbital part of the malar is flattened laterally, not rounded. The lower border of the nasal notch (preserved in the paratype) indicates that this notch extends much farther backward than in *T. ultimum*. The evidence suggests, therefore, that the free portion of the nasals, as in other Mongolian titanotheres, was long, whereas in *T. ultimum* it was distinctly short. The contour of the lower jaw differs profoundly from that of *T. ultimum*, which was far more shallow and wholly without the downward sweep of the lower border. The cheek teeth can all be derived more readily from those of other Mongolian titanotheres by emphasis of certain

characters. In brief, it seems to represent a new genus, which we have named as above. In the extreme anteroposterior elongation of its molars this genus exceeds all other known titanotheres, but in regard to this feature and others the new genus *Dolichorhinoides* (see above) tends to connect *Gnathotitan* with other Mongolian forms in the subfamily Epimanteoceratinae.

POSTSCRIPT.—After renewed and extended comparison, *Gnathotitan* again appears to be a specialized offshoot of the *Protitan* stem. It is in that genus that we find the most favorable points of departure for the great enlargement of the lower incisors, for the elongation of the upper molars (compare *P. grangeri*, Amer. Mus. No. 20108), while *Microtitan* and *Dolichorhinoides* also show stages of specialization in the same direction. The lower premolars and molars present nothing inconsistent with derivation from the same source.

Gnathotitan berkeyi (Osborn)

Plate XIV, figures A, B, C

Telmatherium berkeyi OSBORN, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, p. 8.

HOLOTYPE.—Amer. Mus. No. 20106, a nearly complete lower jaw and right maxilla (Tables VII, IX).

PARATYPE.—Amer. Mus. No. 20121, a maxilla, and probably Amer. Mus. No. 20107, a lower jaw, front half (W. K. G.).

HORIZON AND LOCALITY.—Irdin Manha formation, Irdin Manha.

SPECIFIC CHARACTERS.—Of titanic size, the lower jaw (800 mm. from condyle to incisive border) much exceeding that of any other known titanotheres (*Protitanotherium superbum*, 580; *Menodus giganteus*, 690). Lower jaw extremely deep beneath the cheek teeth (215 mm. beneath m_2), rising steeply to the small spatulate symphysis. P^1-m^3 , 359; p^1-p^4 , 138; m^1-m^3 , 235; index, $(p^1-p^4) \times 100 \div (m^1-m^3) = 58$. M^3 excessively elongate anteroposteriorly (pas. to mts., 112 mm.; pr. ms., 71; breadth index, 63). P^2 , p^3 , p^4 all very advanced, each with two subequal external cusps, subquadrate inner border and low tetartocone ridge which is extended to the posterior cingulum. P^1 simple but with

marked posterointernal pit. Upper canine with extremely swollen root and recurved tip. The infraorbital canal (in the "paratype," Amer. Mus. No. 20121) opens far in front of the orbit, above the posterior end of p^4 . Anterior end of the malar beneath the orbit flattened externally with a rounded lower margin, much as in *Protitan*. P^1-m^3 , 340; p^1-m^3 , 355. For other measurements of the upper teeth see Table VII.

REMARKS.—In Osborn's "paratype" (Amer. Mus. No. 20121) p^2-p^4 are longer anteroposteriorly than those of the type, the outer cusps less subequal and the inner border less quadrate, so that the general appearance is decidedly different. A possible structural ancestor of *Gnathotitan* but from the same level and locality is represented by Amer. Mus. No. 20125, a fragment including p^1-p^3 , left. The ectolophs of p^2 , p^3 are remarkably oblique, the inner ridge and cusp of p^3 strongly developed; apparently traces of this condition are seen in a maxilla, Amer. Mus. No. 20121, Osborn's paratype of "*Telmatherium berkeyi*."

RHINOTITAN, NEW GENUS

GENOTYPE.—*Dolichorhinus kaiseni* Osborn, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, p. 9.

REFERRED SPECIES.—*Protitanotherium andrewsi* Osborn, *Protitanotherium mongoliense* Osborn.

GENERIC CHARACTERS.—Mongolian Epimanteoceratinae of the Shara Murun formation, of moderate to large size; nasals long, more or less upturned, subnasal pillars strong; naso-frontal horns small, oval; occiput wide, but little extended behind the condyles; auditory meatal groove partly closed below; upper incisors and canines moderate or large, postcanine diastema retained. Upper premolars highly progressive, with more or less distinct tetartocone ridges; upper molars of widely varying proportions but at most moderately elongated; lower incisors large, lower canines large but often showing tendency to join the incisor series; lower postcanine diastema pronounced; p_2 moderately progressive, often with metaconid; lower molars moderately elongate, the measurement m_1-m_3 being about one-third that of the incisive alveoli to condyle; p_2-p_4 wider and more advanced than those of *Protitanotherium emarginatum* but not very different from those of *P. superbum*; symphysis much narrower than in the latter.

REMARKS.—The type species of this

genus resembles the American form *Dolichorhinus* in its long nasals, small oval nasofrontal horns, long skull top; but it differs widely from the latter in its spreading short occiput, in the extreme forward position and relative lateral protrusion of the horns, in the forward tapering of the opposite zygomata as seen from above, in the shortness and downward curvature of the premaxillae in side view, in the much greater breadth and size of the cheek teeth, and many other features, in nearly all of which *Rhinotitan* shows close relationships with *Protitan grangeri* and *P. robustus*, of which it may indeed be a descendant. In short, the nearer relationships of *Rhinotitan* are indubitably closer to the other Mongolian titanotheres than to the American *Dolichorhinus*.

Rhinotitan kaiseni (Osborn)

Plate xv, figures A, B, C

Dolichorhinus kaiseni OSBORN, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, p. 9.

TYPE.—A skull and jaws, Amer. Mus. No. 20252.

PARATYPE.—“A palate and basicranium” (Amer. Mus. No. 20257).

HORIZON AND LOCALITY.—Shara Murun formation, Ula Usu.

SPECIFIC CHARACTERS.—General dimensions smaller and p^4 relatively much wider than in *Rhinotitan mongoliensis* or *R. andrewsi*; upper molars the same.

REMARKS.—The relationship of *R. kaiseni* to *R. mongoliensis* and *R. andrewsi* seems to be very close in spite of dimensional differences. The general morphology of the skull is practically the same, as is the stage of evolution of the upper and lower premolars. Indeed the material already available (partly noted in Tables X and XI) indicates that these three supposed species form a continuous series both in size and evolutionary stages of the dentition. Nevertheless it is convenient to retain the three specific names at least for the type and paratype specimens.

Rhinotitan mongoliensis (Osborn)

Plate xvi, figures A, B, C

Protitanotherium mongoliense OSBORN, Amer. Mus. Novitates, No. 91, Oct. 17, 1923, p. 3.

HOLOTYPE.—Amer. Mus. No. 18653, an incomplete right mandibular ramus, containing well preserved p_2 - m_3 (Table XI).

HORIZON AND LOCALITY.—Shara Murun beds, Ula Usu.

NEOTYPE.—Amer. Mus. No. 20263, a palate (σ) with complete dentition (Table X).

REFERRED SPECIMENS.—Amer. Mus. Nos. 20261, a laterally crushed female (?) skull; 20256, a palate (see also lower jaw below); 20270, right maxilla; 21598, palate with p^1 - p^3 , dp^4 , m^1 , m^2 ; lower jaws, 20273, 20256, 21605, probably also 20272.

SPECIFIC CHARACTERS.— P^2 - p^4 in neotype with tetartocones less distinct from the deutocone crest than in the type of *R. andrewsi*.

REMARKS.—The type lower teeth present many resemblances to those of the American forms *Protitanotherium emarginatum* and *P. superbum*, as noted by Osborn, yet they are still closer to those of other Mongolian titanotheres, such as *Protitan robustus*, while the very large incisors and canines (not shown in the type lower jaw) do not favor the reference of this species to the American genus. The relationship of *mongoliensis* with *andrewsi* is close and the differences between extremes both in the stages of evolution and in the dimensions are bridged by several specimens which make a continuous series and raise grave doubt as to the distinctness of the two species.

Rhinotitan andrewsi (Osborn)

Plate xvi, figure D

Protitanotherium andrewsi OSBORN, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, p. 6.

HOLOTYPE.—Amer. Mus. No. 20271, a skull with complete dentition but lacking the nasal region (Table X).

HORIZON AND LOCALITY.—Shara Murun beds, Ula Usu.

PARATYPE.—Amer. Mus. No. 20251, a lower jaw from the same locality and horizon (Table XI).

The “specific distinctions” from “*Protitanotherium mongoliense*” noted by Osborn (1925, p. 6) do not hold good with the larger series of specimens now at hand. It is true that the type of *P. andrewsi*, as

compared with the neotype of *R. mongoliensis*, is somewhat larger, that the tetartocones of its p^2 , p^3 are more distinct and that it has a minute "hypocone" (?) on m^3 , but apart from the last named character these differences are bridged by other specimens. Nevertheless we tentatively retain the name *andrewsi* for the more progressive stage of the apparently continuous series represented by the names *Rhinotitan kaiseni*, *R. mongoliensis* and *R. andrewsi*.

REMARKS.—The lower jaw differs from that of the American *Protitanotherium* in its very large incisors, while the skull has a very wide flattened occiput which foreshadows those of the Mongolian genera *Parabrontops* and *Metatitan*.

PACHYTITAN, NEW GENUS

GENOTYPE.—*Pachytitan ajax*.

GENERIC CHARACTERS.—Gigantic Epimanteoceratinae of Shara Murun (upper Eocene) age, with massive, upturned, bluntly tipped nasals supported by great convex subnasal pillars which tend to constrict the upper part of the nasal chamber; naso-frontal horns relatively large (for a Mongolian titanotherine) with elongate oval base. Incisors and canines of fairly large size, a moderate postcanine diastema, upper premolars advanced, with strong tetartocones, third upper molar broad.

Pachytitan ajax, new species

Plate XVII, figure A

HOLOTYPE.—Fore part of skull (Amer. Mus. No. 21612). See Table XII.

HORIZON AND LOCALITY.—Shara Murun beds, four miles north of Baron Sog Lamasery, Shara Murun region.

SPECIFIC CHARACTERS.—Size very large, extreme length of left horn base, 203 mm., height, 100 mm., nasal notch, about 220 mm.; p^2 - m^3 relatively short (about 300 mm. est.), p^2 - p^4 large, squarish, with well advanced tetartocones (p^2 - p^4 , 98 mm.), postcanine diastema, 38 mm., m^3 crushed but apparently wide; upper incisors and canines of moderate size; nasals bluntly pointed, with massive subnasal pillars.

REMARKS.—This animal is fairly close to *Rhinotitan andrewsi* in the form and measurements of its upper cheek teeth, but its skull is too large to go with the lower jaw of that species. Its massive sharply upturned and somewhat tapering nasals differ considerably from those of *Rh. mongoliensis* (the nasals are unknown in the type of *Rh. andrewsi*). It is probably not con-

generic with *Titanodectes*, for in that form the lower incisors appear to be much too wide and the lower canine too small to be associated with the present skull, while the third lower molar of *Titanodectes* is much too large.

PARABRONTOPS, NEW GENUS

GENOTYPE.—*Brontops gobiensis* Osborn.

GENERIC CHARACTERS.—Extremely broad skulled and specialized Epimanteoceratinae of the Ardyn Obo (= ?Ulan Gochu) formation. Nasals very wide, shorter than in *Metatitan*, with short subnasal pillars which do not constrict the upper part of the nasal chamber; naso-frontal horns prominent, swollen, with anteroposteriorly oval bases and low rounded summits, located above and slightly in front of the orbits; skull as seen from below more or less triangular, occiput very wide, projecting but little behind occipital condyles; zygomatics deep and thick, buccal expansions lateral to preglenoid eminences rather than anterior to them; postzygomatic vertical swellings thick; auditory groove bordered below by narrow contact of posttympanic with postglenoid process. Upper incisors three on each side, very small (represented by alveoli in the type). Canines not large even in supposed males. Upper cheek teeth with wide m^3 and highly progressive premolars, the tetartocones of p^3 , p^4 large, prominent and circular, with or without a narrow isthmus connecting them with the deuterococones; internal cingula of premolars conspicuous, external cingula lacking; p^1 advanced, with incipient second lobe and large posterointernal swelling; lower jaw with massive swollen symphysis, massive rami (corpus mandibulae), relatively low condyles and rather delicate coronoid processes; i_3 relatively small, lower canines large or small, with or without swollen roots. Pachyostosis incomplete, affecting chiefly the naso-frontal horn swellings, the posterior part of the zygomatic and the mandible.

REMARKS.—This differs widely from the true *Brontops* of North America in many of the characters noted above. It is seen to be a direct offshoot of such older Mongolian genera as *Rhinotitan* or *Protitan*, with which it agrees in the short, very wide occiput, subtriangular form of skull as seen from above, posterior position of lateral zygomatic swellings, presence of posterior vertical zygomatic swellings and the like. Relationships of *Parabrontops* with *Metatitan* are also close, the principal differences being the much greater size of the horns and the lesser width of the premaxillary incisal border.

Parabrontops gobiensis (Osborn)

Plate xvii, figure B; Plate xviii, figures A, B;
Plate xix, figures A, B

Brontops gobiensis OSBORN, Amer. Mus. Novitates, No. 202, Nov. 24, 1925, p. 5.

HOLOTYPE.—Amer. Mus. No. 20354, a badly crushed skull (Table XIII).

HORIZON AND LOCALITY.—Ardyn Obo beds, Ardyn Obo.

REFERRED SPECIMENS.—Amer. Mus. No. 26020, a skull, lacking the basicranium, from Urtyn Obo; Amer. Mus. No. 26019, a fine lower jaw with very small incisors, also from Urtyn Obo; Amer. Mus. No. 26131, a lower jaw from Spring Camp, East Mesa, Shara Murun region (Tables XIII, XIV).

SPECIFIC CHARACTERS.—Not yet distinguished from generic characters.

REMARKS.—The excellent reconstruction of the type skull, made by Mrs. L. M. Sterling under Osborn's direction, when viewed in the light of material now available serves to emphasize the relatively close relationship of this form with *Metatitan*, the main differences being that in *Parabrontops* the pachyostosis of the horns is much more pronounced, and there is no suggestion of a connecting crest. In the referred skull (No. 26020) there are in all four incisor alveoli, which probably represent i^3 , i^2 on each side, but the alveoli of the medial pair of incisors (i^1), if formerly present, are not evident, and the teeth in any event must have been very small. Thus *Parabrontops* may have been approaching the condition seen in the American *Brontops* in which the number of incisors was reduced to $\frac{2}{2}$.

METATITAN, NEW GENUS

GENOTYPE.—*Metatitan relictus*.

GENERIC CHARACTERS.—The last of the Epi-manteoceratinae: skulls widening posteriorly to the extremely broad low occiput; nasals very wide and long, not or but moderately upturned, bearing small knob-like naso-frontal horns supported by slight subnasal pillars; buccal expansions slight, located at the posterior end of the zygomata, vertical postzygomatic swellings pronounced; premaxillary incisal border flattened and widened, the opposite upper canines widely separated; premaxillo-maxillary rostrum shortened in front; incisors, small; upper pre-

molars crowded, the postcanine diastema reduced; p^1 small but with complex crown; premolar tetartocones typically advanced; internal cingula strong; upper molars moderately wide with relatively advanced accessory details (small anterior and posterior cement lakes, slightly wrinkled enamel, etc.); occipital base short, audital groove closed below; lower jaw with swollen symphysis; i_3 small, lower postcanine diastema reduced, lower premolars relatively advanced, m_3 moderately elongate.

REMARKS.—These curiously specialized forms were among the last members of their great family. They were undoubtedly derived from *Rhinotitan* and carried further its peculiar widening of the occiput, but they retained to the last the primitive number of incisors and never enlarged their naso-frontal horns. The suggestion that *Metatitan* might be the female of *Embolotherium* is not supported by the fact that while some *Metatitan* have small canines, others have relatively large canines and stout zygomatic arches. Nevertheless the cheek teeth of the two genera indicate relatively close relationship to each other and the at first sight unbridgeable differences in the "horns" appear to be mediated by certain specimens described below.

Metatitan primus, new species

Plate xx, figures A, B, C; Plate xxi, figures A, B

HOLOTYPE.—Amer. Mus. No. 26101, a well preserved skull and jaw (Tables XIII, XIV).

HORIZON AND LOCALITY.—?Ulan Gochu formation, Chimney Butte, North Mesa, Shara Murun region.

SPECIFIC CHARACTERS.—Nasals large and relatively short with large down turned edges and but slight subnasal pillars; naso-frontal horns relatively prominent, located well in front of the orbits, their summits joined by a transverse convexity, which slopes downward to the midcranium. A very large median parietal eminence in the type skull; upper and lower canines relatively large in type; lower incisors very small (i_1), small (i_2) or medium (i_3).

REMARKS.—This important form is plainly related to *Parabrontops* but differs in that pachyostosis has not greatly affected the paired horns; on the other hand, it points the way to *Embolotherium*, since its horns are displaced forward in front of the orbit and joined by a transverse connecting crest. Its relationships with *Metatitan relictus* are obviously close.

Metatitan progressus, new species

Plate XXII, figures B, C; Figure 7A, B

HOLOTYPE.—Amer. Mus. No. 26014, front part of right side of skull, with nasal "horn," orbit and p^4 , m^1 .

HORIZON AND LOCALITY.—Ulan Gochu formation, Jhama Obo, East Mesa, Shara Murun region.

SPECIFIC CHARACTERS.—Horns very prominent in side view, joined by a steep connecting

of *Embolotherium* has been derived in the manner suggested on page 370, for in this specimen the proximal margins of the nasal bones are already being overtopped by the forwardly moving "horns" and their transverse connecting crest. *Metatitan progressus* is, however, closely related to *M. relictus* and may eventually be connected with it by intergrading specimens.

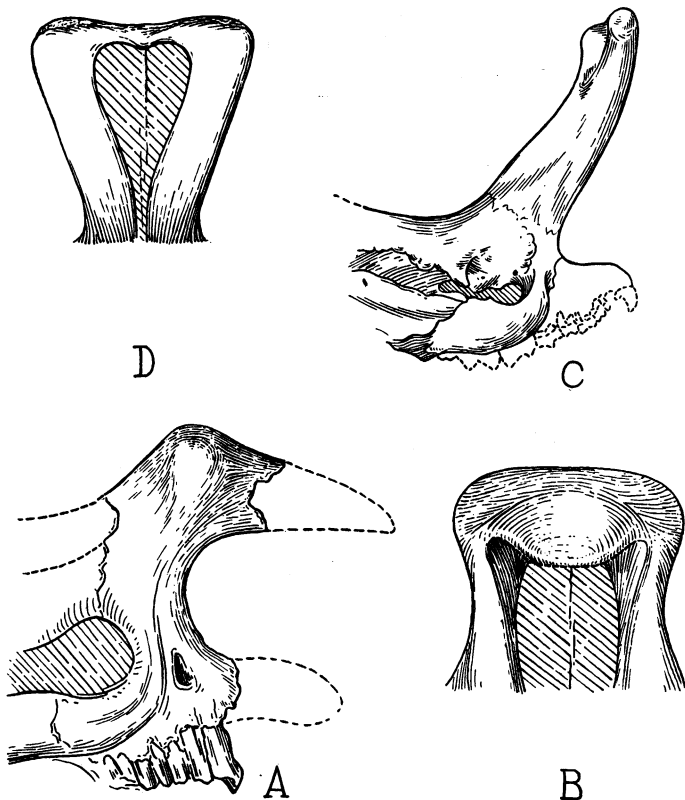


Fig. 7. Comparison of nasal horn region in *Metatitan progressus* (A, B) and *Embolotherium andrewsi* (C, D). A, B, ca. $\frac{1}{8}$, C, ca. $\frac{1}{15}$, D, ca. $\frac{1}{15}$ natural size.

crest which is even higher than the horns as it nears the mid-line, nasal roof sloping downward from the connecting crest, posteroinferior lateral border of nasals sloping upward, nasal notch extending far backward to a point a little above and in front of the infraorbital foramen; pachyostosis prominent at least in horns, connecting crest, preorbital border and suborbital part of zygomatic arch.

REMARKS.—The type specimen, although very strange at first sight, furnishes important evidence that the nasal "ram"

Metatitan relictus, new species

Plate XXI, figures C, D; Plate XXII, figure A; Plate XXIII; Plate XXIV, figures A, B

HOLOTYPE.—Amer. Mus. No. 26391, skull and lower jaws (Tables XIII, XIV).

HORIZON AND LOCALITY.—Houldjin formation, Camp Margetts.

REFERRED SPECIMENS.—Amer. Mus. Nos. 26395, 26396, 26397, 26398, 26399, skulls from the same general locality and horizon; Amer. Mus. No. 26406, a left maxilla with i^2 - m^2 :

lower jaws, Amer. Mus. Nos. 26404, 26400 (?), 26402.

SPECIFIC CHARACTERS.—Horns delicate, low, with or without transverse connecting crest; horns tending to project laterally beyond nasal rim, the latter delicate; nasal tip slightly de-curved; pachyostosis not conspicuous in horn region; canines large in supposed males, i^1 , i^2 very small, i^3 larger; lower jaw but little expanded; lower cheek teeth small, with wide space between m_2 and coronoid process; lower incisors fairly small, subequal, forming a transverse row; upper and lower premolars advanced, crowded.

REMARKS.—*Metatitan relictus*, although one of the latest titanotheres, escaped the extreme specializations that were associated with pachyostosis and extreme forward movement of the horns.

Metatitan species

A jaw which may be provisionally referred to *Metatitan* species is Amer. Mus. No. 26407, likewise from Camp Margetts and from a level which was doubtfully marked ?Houldjin. This jaw has the progressive p_2 - p_4 of *Rhinotitan* and *P. ? cingulatus* combined with the delicate dimensions of *Protitan minor*. The external cingula, however, are much less prominent than in *P. ? cingulatus*.

Embolotheriinae Osborn

Skull brachycephalic with zygomata widely expanded in the middle; "horns" greatly displaced forward and together with the connecting crest between them forming a huge upturned nasal ram; tip of nasal bones reduced or vestigial, overhung by connecting crest; auditory groove closed below. Second and third upper molars very wide, upper and lower premolars advanced; third lower molar very large, elongate, with heavy external cingula.

- A. Lower front teeth eight, very large even in old individuals, arranged in a broad forwardly directed scoop, including six incisors and two canines of the permanent dentition . . . *Titanodectes*.
- AA. Lower front teeth six, very small even in old individuals, consisting of retained deciduous incisors arranged in a spatulate series, the permanent incisors very large but remaining unerupted in the jaw; canines very small

Embolotherium.

TITANODECTES, NEW GENUS

GENOTYPE.—*Titanodectes ingens*.

GENERIC CHARACTERS.—Large to gigantic Embolotheriinae of Shara Murun and Ulan Gochu age, with eight large lower front teeth in a slightly curved row, the outermost pair being canines; m_2 of enormous size; lower molars and premolars with heavy external cingulum.

REMARKS.—*Titanodectes* is in certain respects intermediate between *Rhinotitan* and *Embolotherium*. A certain jaw (Amer. Mus. No. 21600) presents an interesting mixture of characters. Unfortunately *Titanodectes* is known only from the lower jaw, but, at least in *Titanodectes ingens*, the skull was probably not unlike that of *Embolotherium*.

Titanodectes minor, new species

Plate xxv, figure D

HOLOTYPE.—Amer. Mus. No. 26132, an incomplete lower jaw with front teeth and p_2 - m_1 (Table XIV).

HORIZON AND LOCALITY.—Shara Murun.

PROVISIONALLY REFERRED SPECIMENS.—Two incomplete lower jaws recorded from Ulan Gochu (Amer. Mus. Nos. 26021, 26012) and one from Shara Murun (Amer. Mus. No. 21600). See Table XIV.

SPECIFIC CHARACTERS.—Six large incisors essentially similar to those of *Rhinotitan* but larger, associated with procumbent canines that may be retained deciduous canines, the incisors and canines collectively suggesting those of *Titanodectes ingens* but smaller. Pachyostosis strongly affecting the symphyseal region and the ramus (corpus mandibulae); medial incisors (i_1) much smaller than i_2 ; lower premolars well advanced in stage.

REMARKS.—In the type jaw there are two large teeth embedded which appear to be unerupted permanent canines. On the other, hand the tooth which is planted in plaster next to the incisors seems to be too large to belong to the deciduous set. In any event this specimen is intermediate in character between *Rhinotitan* and *Titanodectes ingens*. We may provisionally refer to this species a lower jaw, Amer. Mus. No. 26021, from Urtyn Obo, with p_1 - m_3 and several front teeth. The latter are close to those of the type, but p_2 , p_3 are distinctly narrower. On the other hand, this specimen is close to the type of *Rhinotitan mongoliensis*, save that its p_3 , p_4 are smaller.

Taken together these two specimens (Amer. Mus. Nos. 26132, 26021) serve to

emphasize the fact that *Titanodectes* tends to connect the stem of the embolotheres with *Rhinotitan*, a conclusion fully supported by other evidence (see Table XIV).

Titanodectes ingens, new species

Plate xxv, figures A, B, C

HOLOTYPE.—Amer. Mus. No. 26005, a large lower jaw with eight front teeth and much worn p_1-m_2 (Table XIV).

HORIZON AND LOCALITY.—Jhama Obo, East Mesa, Shara Murun.

SPECIFIC CHARACTERS.—Lower incisors very large, associated with relatively small procumbent lower canines, lower m_3 very large, much like that of *Embolotherium*.

REMARKS.—The lower cheek teeth are so like those of *Embolotherium* that relatively close relationship can hardly be denied. The permanent incisors, which are of exceptionally large size, are like those of *Titanodectes minor*.

An isolated m_2 (Amer. Mus. No. 20351) from Ardyn Obo, the type of *Menodus mongoliensis* Osborn, probably pertains to *Titanodectes ingens* or *Embolotherium* species.

EMBOLOTHERIUM OSBORN

GENOTYPE.—*Embolotherium andrewsi* Osborn.

GENERIC CHARACTERS.—Skull top running forward and upward into a huge bony ram. Occiput surmounted by enormous lambdoidal crests which project far behind the condyles. Front teeth belonging to the deciduous series and very small even in old individuals; supported on small spatulate incisal portions of the premaxillae and lower jaw. Permanent upper and lower incisors very large but impacted or unerupted in the jaws. Zygomatic with enormous buccal swellings, located in front of the glenoid eminences; cheek teeth progressive, m^3 enormous and very broad, m_3 very long, lower molars with strong external cingula.

REMARKS.—The type of *Menodus? mongoliensis* Osborn from the Ardyn Obo is a very large m_2 which agrees very closely with those of jaws referred to either *Titanodectes ingens* or *Embolotherium andrewsi*. In view of the doubt, however, *Menodus? mongoliensis* may be regarded as a practically indeterminate species. In any event

the reference to the American genus *Menodus* is improbable, because neither *Titanodectes* nor *Embolotherium* appears to be closely related to *Menodus*.

Embolotherium andrewsi Osborn

Plate xxvi, figures A, B, C; Plate xxvii, figures A, B, C; Plate xxviii, figures A, B; Plate xxix

Embolotherium andrewsi OSBORN, Amer. Mus. Novitates, No. 353, May 30, 1929, p. 13.

HOLOTYPE.—Amer. Mus. No. 26001, a skull with maxillary rostrum wanting.

HORIZON AND LOCALITY.—Ulan Gochu formation.

REFERRED SPECIMENS.—Amer. Mus. Nos. 26000, a well preserved skull presented to the Chinese Geological Survey Museum; 26010, perfect palate and base of skull; 26003, a fine skull; 26004, another nearly perfect skull; 26009, skull and lower jaws; lower jaws, 26006, 26011; doubtfully referred, 21600, 26008 (Tables XV, XVI).

SPECIFIC CHARACTERS.—Dorsal contour of ram strongly concave, premaxillary rostrum very small.

REMARKS.—It was supposed by Osborn that the great bony ram of *Embolotherium* had nothing to do with the paired horns of other titanotheres, but that it was a structure *sui generis*, which at once separated the embolotheres from all other known forms and made them the type of a new subfamily of unknown derivation. A study of the material now available, however, has led one of us (W. K. G.) to widely different conclusions, namely: (a) that the "ram" of *Embolotherium* represents only an extreme development of tendencies observed in other Mongolian genera; (b) that it has arisen through the forward and upward immigration of the paired horns; (c) that the connecting crest between the horns grew forward and upward with them to such an extent that it finally overhung the tip of the nasals; (d) that the median tip of the nasals gradually turned downward and its free portion became absorbed as the transverse connecting crest gradually overshadowed it (see Fig. 7).

Embolotherium is also connected with other Mongolian titanotheres by the genus *Titanodectes* (see p. 369 above).

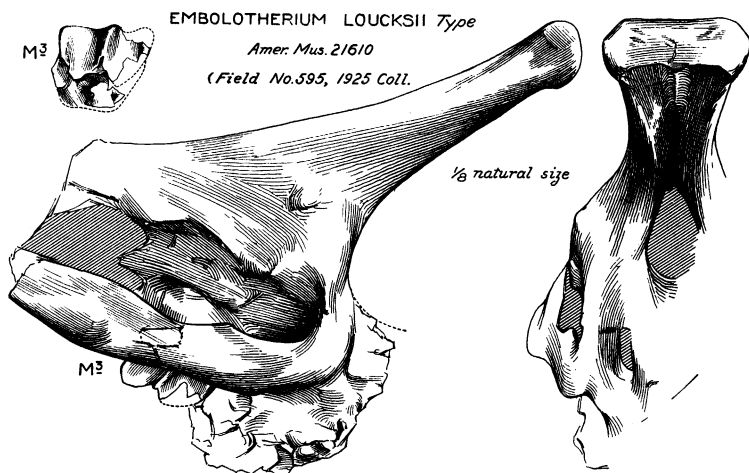


Fig. 8. *Embolotherium loucksii*, holotype, after Osborn, $\frac{1}{8}$ natural size.

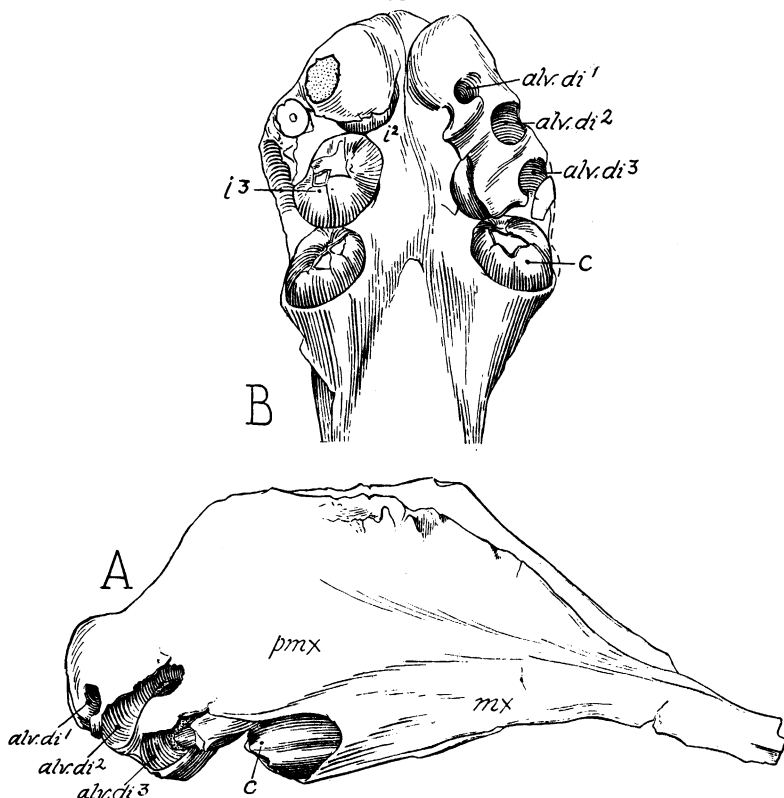


Fig. 9. Premaxillary and presumably part of maxillary of *Embolotherium loucksii*, $\frac{3}{4}$ natural size.

Embolotherium loucksii Osborn

Figures 8-11 and Plate xxx, figures A, B, C

Embolotherium loucksii OSBORN, Amer. Mus. Novitates, No. 353, May 30, 1929, p. 16.

TYPE.—Amer. Mus. No. 21610, front portion of skull with nasal "ram."

HORIZON AND LOCALITY.—Ulan Gochu formation, four miles north of Baron Sog.

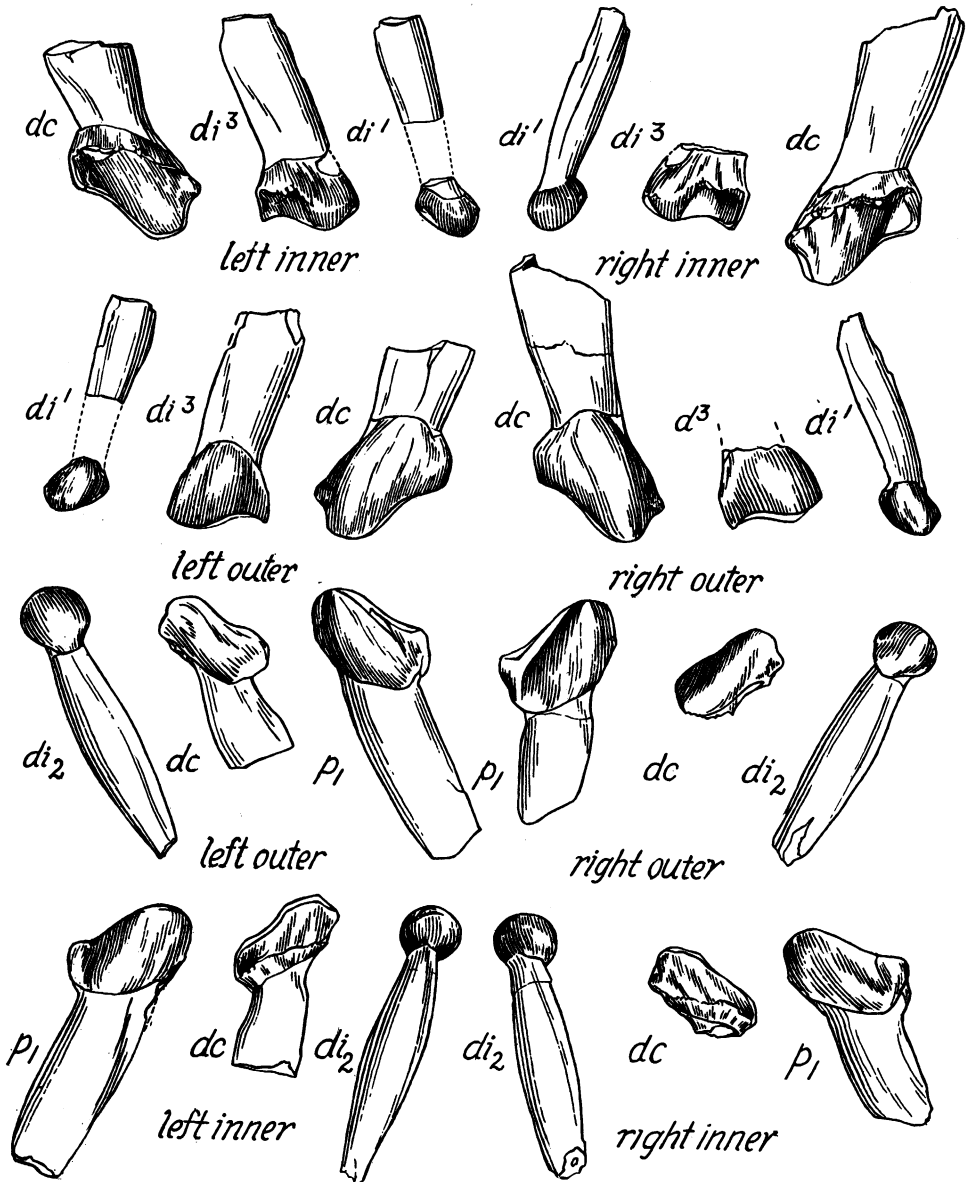


Fig. 10. Deciduous front teeth (incisors, canines and p_1) of *Embolotherium loucksii*, natural size.

REFERRED SPECIMEN.—Amer. Mus. No. 26040, a juvenile skull and jaws.

SPECIFIC CHARACTERS.—Dorsal contour of nasal ram nearly straight, free border of nasals a transverse rim beneath the overhanging connecting crest. Horns rep-

resented by rounded projecting corners of connecting crest.

REMARKS.—The condition of the nasal ram is much less advanced than in *Embolotherium andrewsi*. The upturning of the nasals is distinctly foreshadowed in *Rhino-*

titan, *Pachytitan* and *Metatitan*. The front view of the type, when compared with that of *Metatitan progressus*, supports the conclusion that the paired horns are represented by the lateral tips of the connecting crest.

deciduous incisors and canines, five pairs and two odd teeth are preserved, but their proper arrangement in the upper and lower jaws is very difficult. They vary greatly in size of crown, some being small rounded

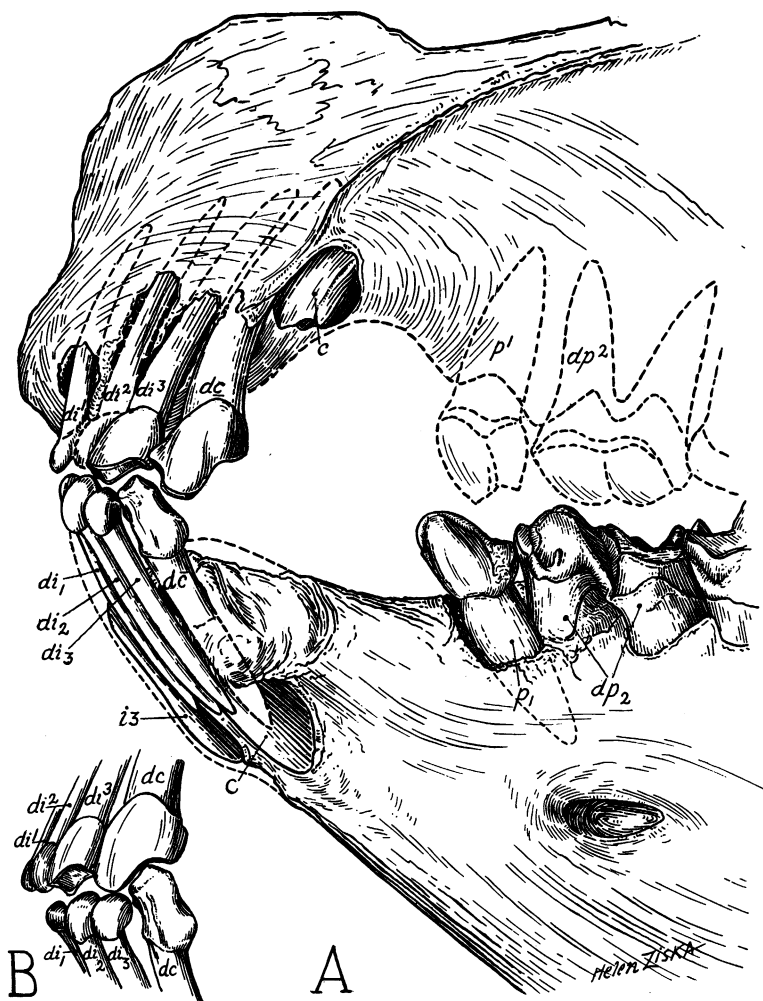


Fig. 11. Restoration of front part of jaws and teeth of *Embolotherium loucksii*. A, Mandible protracted and lower canine in contact with di^3 , dc. B, Mandible retracted and lower deciduous canine articulating with posterior slope of upper deciduous canine. $\frac{3}{4}$ natural size.

The juvenile specimen (Amer. Mus. No. 26040) referred by Osborn to *E. grangeri* seems to us much closer to *E. loucksii*. This specimen has very large unerupted front teeth embedded in both the upper and lower jaws and tends to connect *Embolotherium* with *Titanodectes*. Of the

nubbins like shoe buttons, others having crowns three or four times as large and with well developed tips, crests and internal cingula. After many trials one of us (W. K. G.) worked out the arrangement shown in Figs. 9, 10, 11.

Embolotherium (?) grangeri Osborn

Embolotherium grangeri OSBORN, Amer. Mus. Novitates, No. 353, May 30, 1929, p. 14.

HOLOTYPE.—Amer. Mus. No. 26002, a skull (Table XV).

HORIZON AND LOCALITY.—“Middle red beds,” Ulan Gochu, East Mesa.

SPECIFIC CHARACTERS.—Dorsal contour of nasal ram strongly convex, premaxillary rostrum unreduced.

REMARKS.—This form differs from *E. loucksii* in the strongly convex dorsal contour of its nasal ram, which is straight in the latter species. It may conceivably represent the skull of *Titanodectes ingens*.

The skull, Amer. Mus. No. 26004, referred to this species by Osborn seems to belong with *E. andrewsi*.

Embolotherium ultimum, new species

Plate xxxi

HOLOTYPE.—Amer. Mus. No. 21604, a posterior portion of base of skull with m^2 , m^3 ,

right, and lambdoidal crests and zygomatic arches (Table XV).

HORIZON AND LOCALITY.—Baron Sog beds (Houldjin), four miles north of Baron Sog, Shara Murun region, Inner Mongolia.

SPECIFIC CHARACTERS.—Size in old male type exceeding that of all Ulan Gochu forms. M^1 of great size and relative width; m^2 relatively smaller; buccal expansions of zygomatic and occipital and lambdoidal crests extreme.

REMARKS.—This is the only titanotherium from the typical Baron Sog beds. The other titanotheres from this horizon are from the equivalent Houldjin beds far to the north of this locality (Table XVI).

Embolotherium species

What proves to be a fragment of the occipital crests of an undetermined species of *Embolotherium* (Amer. Mus. No. 20352) was found in the Ardyn Obo beds. The reference to *Embolotherium* is unquestionable, and this furnishes additional evidence of the equivalence of the Ardyn Obo with the Ulan Gochu beds.

TABLE I.—COMPARATIVE MEASUREMENTS OF *Telmatherium*, *Manteoceras* AND *Metatelmatherium*

	<i>Telmatherium cultridens</i> Type, From east of Princeton Museum No. 1027	" <i>Manteoceras manteoceras</i> " Bridger Eocene, Amer. Mus. No. 12683	<i>Metatelmatherium ultimum</i> Type, Uinta? B. Amer. Mus. No. 2060	<i>Metatelmatherium cristatum</i> Type, Irwin Manha. Amer. Mus. No. 26411
(3) Cheek teeth length (p^1 - m^3) middle	180	175	218	233
(4) p^1 - p^4 length (middle)	80	74.5	90	92
(5) m^1 - m^3 length (middle)	103	100	129	140
III. Index: $(p^1-p^4) \times 100 \div (m^1-m^3)$	77%	74%	69%	65%
(6) Diastema, post. surf. canine to p^1	10	9	17	22
(7) m^3 length (parast. to mts.)	44	41	56	54
(8) m^3 width (pr. to mesost.)	40	41	58	56
V. Index: m^3 width $\times 100 \div m^3$ length	90%	100%	103%	103%
(9) m^2 length (pas. to mts.)	43	40	48.5	53.5
(10) m^2 width (pr. to ms.)	39	38	55	56
VI. Index: m^2 width $\times 100 \div m^2$ length	90%	95%	113%	104%
(11) m^1 length (pas. to mts.)	31	29	37	40.5
(12) m^1 width (pr. to ms.)	30	30	44	43
VII. Index: m^1 width $\times 100 \div m^1$ length	96%	103%	118%	106%
(13) p^4 length	23	20	25	26
(14) p^4 width	26	24	35	32
VIII. Index: p^4 width $\times 100 \div p^4$ length	113%	120%	140%	123%
(15) i^1 transverse, at base of crown	...	10	14	...
(16) i^2 transverse, at base of crown	12.5	12	15	17
(17) i^3 transverse, at base of crown	16	16	18	21

TABLE II.—COMPARATIVE MEASUREMENTS OF *Metatelmatherium cristatum* AND *M. ultimum*

	<i>Metatelmatherium cristatum</i> Type. Irwin Manha. Amer. Mus. No. 28411	<i>Metatelmatherium ultimum</i> Type. Amer. Mus. No. 2060
(1) Basal length (L) pmx. to condyle	585	510
(2) Transverse zygomata (tr.)	330	300
I. Index: $\text{tr.} \times 100 \div \text{L}$	56%	58%
(3) Cheek teeth length (p^1 to m^3) middle	233	218
II. Index: $(p^1 - m^3) \times 100 \div \text{L}$	39%	42%
(4) $p^1 - p^4$ length (middle)	92	90
(5) $m^1 - m^3$ length (middle)	140	129
III. Index: $(p^1 - p^4) \times 100 \div (m^1 - m^3)$	65%	69%
IV. Index: $(m^1 - m^3) \times 100 \div \text{L}$	23%	25%
(6) Diastema, post. surf. canine to p^1	22	17
(7) m^3 length (parast. to mts.)	54	56
(8) m^3 width (pr. to mesost.)	56	58
V. Index: $m^3 \text{ width} \times 100 \div m^3 \text{ length}$	103%	103%
(9) m^2 length (pas. to mts.)	53.5	48.5
(10) m^2 width (pr. to ms.)	56	55
VI. Index: $m^2 \text{ width} \times 100 \div m^2 \text{ length}$	104%	113%
(11) m^1 length (pas. to mts.)	40.5	37
(12) m^1 width (pr. to ms.)	43	44
VII. Index: $m^1 \text{ width} \times 100 \div m^1 \text{ length}$	106%	118%
(13) p^4 length	26	25
(14) p^4 width	32	35
VIII. Index: $p^4 \text{ width} \times 100 \div p^4 \text{ length}$	123%	140%
(15) i^1 transverse, at base of crown	Missing	14
(16) i^2 transverse, at base of crown	17	15
(17) i^3 transverse, at base of crown	21	18
(20) Width across posttympanic processes	192	180
XI. Index: $\text{width (20)} \times 100 \div \text{L}$	32%	15%

TABLE IV.—COMPARATIVE MEASUREMENTS OF *Desmatotitan*

	<i>Telmatherium cultridens</i> Type, Princeton Mus. No. 1027	<i>T. cultridens</i> Amer. Mus. No. 1560	<i>Desmatotitan tukhumensis</i> Type, Irdin Manba (Ulan Shueh), Amer. Mus. No. 21606	<i>Metatelmatherium ultimum</i> Type, Amer. Mus. No. 2060	<i>Metatelmatherium cristatum</i> Type, Irdin Manba, Amer. Mus. No. 26411
(23) Length incisor alveoli to condyle (Lmd)	...	353	480
(24) Height condyle to angle (Hmd)	...	132e.	...	196e.	185e.
XII. Index: $Hmd \times 100 \div Lmd$...	37%	38%
(25) Depth below middle of m_3 (Hmd)	65	58	90	93	100
XIII. Index: $Hmd \times 100 \div Lmd$...	16%	20%
(26) Diastema, from canine to p_1	...	14	...	17e.	...
(27) p_1-m_3 length (middle)	...	198	...	252e.	250
XIV. Index: $(p_1-m_3) \times 100 \div Lmd$...	56%	52%
(28) p_1-p_4 length (middle)	...	78	...	96e.	94
(29) m_1-m_3 length (middle)	122	117	144	154	156
XV. Index: $(p_1-p_4) \times 100 \div (m_1-m_3)$...	66%	...	62%	60%
XVI. Index: $(m_1-m_3) \times 100 \div Lmd$...	33%	32%
(30) m_1 length (middle)	29	28	32	38	37
(31) m_2 length (middle)	38	37	47	47	46
(32) m_2 width at talonid	22	21	28.5	29	29
XVII. Index: $m_2 \text{ width} \times 100 \div m_2 \text{ length}$	57%	56%	60%	61%	63%
(33) m_3 length (middle)	53	50	63	68	69
(34) i_1 transverse, at base of crown	15.5	...	11
(35) i_2 transverse, at base of crown	16.5	...	13.5
(36) i_3 transverse, at base of crown	...	13.8	17	...	14.5
(37) p_2-p_4 length (middle)	67	66	73	72e.	76.5

TABLE V.—COMPARATIVE MEASUREMENTS OF *Protitan* AND *Epimanteoceras*

	<i>Protitan minor</i> Ref. Irdin Manha. Amer. Mus. No. 26417	<i>Protitan minor</i> Type, Irdin Manha (Camp Margetta). Amer. Mus. No. 26416	<i>Protitan grangeri</i> Type, Irdin Manha. Amer. Mus. No. 20103	<i>Protitan grangeri</i> Irdin Manha. Amer. Mus. No. 20114	<i>Protitan bellus</i> Type, Irdin Manha (Ulan Shireh). Amer. Mus. No. 26104	<i>Epimanteoceras formosus</i> Irdin Manha. Amer. Mus. No. 21613
(1) Basal length (L) pmx. to condyle	...	542	710	...	710	700
(2) Transverse zygomata (tr.)	...	302	455	...	426	396
I. Index: tr. $\times 100 \div L$...	55%	64%	...	60%	56%
(3) Cheek teeth length (p^1-m^3) middle	234	234	253	250e.	265	249
II. Index: (p^1-m^3) $\times 100 \div L$...	43%	35%	...	37%	35%
(4) p^1-p^4 length (middle)	90	87	93	93	97	94
(5) m^1-m^3 length (middle)	147	151	160	156	170	157
III. Index: (p^1-p^4) $\times 100 \div (m^1-m^3)$	61%	57%	60%	59%	57%	59%
IV. Index: (m^1-m^3) $\times 100 \div L$...	27%	22%	...	23%	22%
(6) Diastema, post. surf. canine to p^1	...	14	39	...	26	23.5
(7) m^3 length (parast. to mts.)	68	65	73.5	79	77	67
(8) m^3 width (pr. to mesost.)	58	57	61	60	64	57
V. Index: m^3 width $\times 100 \div m^3$ length	85%	87%	82%	75%	83%	85%
(9) m^2 length (pas. to mts.)	61	63	67.5	65	74	53
(10) m^2 width (pr. to ms.)	60	52.5	54	52	58	56
VI. Index: m^2 width $\times 100 \div m^2$ length	90%	83%	80%	80%	78%	105%
(11) m^1 length (pas. to mts.)	40	43	43.5	46	50.5	38
(12) m^1 width (pr. to ms.)	47.5	43	42	41	44	42
VII. Index: m^1 width $\times 100 \div m^1$ length	117%	100%	96%	89%	87%	110%
(13) p^4 length	28	30	27	27	32	24.5
(14) p^4 width	39.5	32	33	34	34.5	36
VIII. Index: p^4 width $\times 100 \div p^4$ length	139%	106%	122%	125%	107%	146%
(15) i^1 transverse, at base of crown	...	12	12	...	15	13
(16) i^2 transverse, at base of crown	...	14.5	14.5	...	16	14
(17) i^3 transverse, at base of crown	...	20	18.5	15	22.5	17
(18) Nasals, tip to middle nasal notch	143	...	161	162	...	161
IX. Index: nasal length $\times 100 \div L$	22%	23%
(19) Width across opp. m^3 at mesost.	...	192	200	...	231	194
X. Index: width (19) $\times 100 \div L$...	35%	28%	...	32%	27%
(20) Width across posttym. processes	...	182	256	...	263	227
XI. Index: width (20) $\times 100 \div L$...	33%	36%	...	37%	32%
(21) Lacrimal tubercle to nasal notch	75	50	130	100

TABLE VI.—COMPARATIVE MEASUREMENTS OF *Protitan* LOWER JAWS

	<i>Protitan minor</i> No. 26415 Irdin Manha. Amer. Mus.	<i>Protitan minor</i> No. 26413 Irdin Manha. Amer. Mus.	<i>Protitan minor</i> No. 26418 Houldin. Amer. Mus.	<i>Protitan minor</i> Estimated from Amer. Mus. No. 26416	<i>Protitan minor</i> No. 26410 Irdin Manha. Amer. Mus.	<i>Protitan grangeri</i> Type. Irdin Manha. Amer. Mus. No. 20103	<i>P. grangeri (D. oleus)</i> Type. Irdin Manha. Amer. Mus. No. 20109	<i>Protitan grangeri</i> No. 26408 Irdin Manha. Amer. Mus.	<i>P. grangeri (M. iridimensis)</i> Type. M ₂ not fully up. Irdin Manha. Amer. Mus. No. 20111	<i>Protitan robustus</i> Type. Irdin Manha. Amer. Mus. No. 20104	<i>Protitan robustus</i> No. 20110 Irdin Manha. Amer. Mus.	<i>Protitan robustus</i> No. 20112 Irdin Manha. Amer. Mus.
(23) Length incisor alveoli to condyle (Lmd)	...	475.	402	440	478	569	531	568	532	...
(24) Height condyle to angle (Hmd)	...	200	170	...	213	219	226	230	245	...
XII. Index: $Hmd \times 100 \div Lmd$...	42%	42%	...	44%	38%	42%	40%	46%	...
(25) Depth below middle of m_2 (Hmd)	...	103	95	88	97	...	97	123	105	...
XIII. Index: $Hmd \times 100 \div Lmd$...	21%	19%	15%	18%	21%	19%	...
(26) Diastema, from canine to p_1	26	28	15	...	22	45	25	30	25	...
(27) $pr-m_2$ length (middle)	234	238	241	240	252	268	265	279	273e.	300	294	...
XIV. Index: $(pr-m_2) \times 100 \div Lmd$...	50%	59%	54%	52%	47%	49%	53%	55%	...
(28) $pr-p_4$ length (middle)	76	79	85	90	86	96	93	92	...	100	105	...
(29) m_1-m_2 length (middle)	156	157	188	162	166	172	179	184	...	203	192	195
XV. Index: $(pr-p_4) \times 100 \div (m_1-m_2)$	48%	50%	53%	55%	51%	55%	51%	49%	54%	...
XVI. Index: $(mr-m_2) \times 100 \div Lmd$...	33%	39%	36%	34%	30%	33%	35%	36%	...
(30) m_1 length (middle)	35	34	36	38	35	38	38	40	...	43	44	...
(31) m_2 length (middle)	46	47	47.5	48	49	53	53	53	40	57	59	...
(32) m_2 width at talonid	28	27	28	...	27	30	30	29	29	33	33	32
XVII. Index: m_2 width $\times 100 \div m_2$ length	60%	57%	58%	...	55%	56%	56%	54%	50	55%	55%	53%
(33) m_2 length (middle)	72	75	73	72	80	82	85	86	83	82	91	84
(34) i_1 transverse, at base of crown	14	14.5	17	13	...
(35) i_2 transverse, at base of crown	14	16	16	15.5	19	14.5	13.5
(36) i_3 transverse, at base of crown	14	...	14.5	...	16.5	18	17	21	14.5	14.5
(37) $pr-p_4$ length (middle)	65	69	71	78	72	80	79	79	86e.	87	93	94

TABLE VII.—COMPARATIVE MEASUREMENTS OF *Microtitan*

	<i>Metarhinus fluvialis</i> Type. Amer. Mus. No. 1500	<i>Microtitan mongoliensis</i> Amer. Mus. No. 21611	<i>Epimantoceras formosus</i> Irdin Manha. Amer. Mus. No. 21613	<i>Gnathotitan berkeyi</i> Type. Irdin Manha. Amer. Mus. No. 20106
(3) Cheek teeth length (p^1 - m^3) middle	145	145	249	359
(4) p^1 - p^4 length (middle)	63	57	94	138
(5) m^1 - m^3 length (middle)	84	88	157	235
III. Index: $(p^1-p^4) \times 100 \div (m^1-m^3)$	75%	64%	59%	58%
(6) Diastema, post. surf. canine to p^1	10	9	23.5	48
(7) m^3 length (parast. to mts.)	36	38	67	112
(8) m^3 width (pr. to mesost.)	35	32	57	71
V. Index: m^3 width $\times 100 \div m^3$ length	97%	84%	85%	63%
(9) m^2 length (pas. to mts.)	30e.	35	53	84
(10) m^2 width (pr. to ms.)	34e.	28	56	68
VI. Index: m^2 width $\times 100 \div m^2$ length	113%	80%	105%	80%
(11) m^1 length (pas. to mts.)	...	27	38	64
(12) m^1 width (pr. to ms.)	30e.	23	42	53
VII. Index: m^1 width $\times 100 \div m^1$ length	...	85%	110%	82%
(13) p^4 length	16.5	17	24.5	38
(14) p^4 width	23	18	36	45
VIII. Index: p^4 width $\times 100 \div p^4$ length	139%	105%	146%	118%

TABLE VIII.—COMPARATIVE MEASUREMENTS OF *Microtitan* (CONTINUED)

	<i>Metarhinus fluvialis</i> Amer. Mus. No. 1865	<i>Microtitan mongoliensis</i> Irdin Manha. Amer. Mus. No. 22099	<i>Microtitan mongoliensis</i> Type. Irdin Manha. Amer. Mus. No. 20167
(25) Depth of mandible below m_3	45	64	..
(27) p_1 - m_3 length (middle)	..	160	..
(28) p_1 - p_4 length (middle)	..	57	..
(29) m_1 - m_3 length (middle)	92	103.5	..
XV. Index: $(p_1-p_4) \times 100 \div (m_1-m_3)$..	55%	..
(30) m_1 length (middle)	22	24	23.5
(31) m_2 length (middle)	28	30	..
(32) m_2 width at the talonid	16.5	15.5	..
XVII. Index: m_2 width $\times 100 \div m_2$ length	58%	51%	..
(33) m_3 length (middle)	41	48	..

TABLE IX.—COMPARATIVE MEASUREMENTS OF *Gnathotitan*

	<i>Metalmatherium ultimum</i> Type. Amer. Mus. No. 2060	<i>Protitan grangeri</i> Type. Irdin Manha. Amer. Mus. No. 20103	<i>Gnathotitan berkeyi</i> Type. Irdin Manha. Amer. Mus. No. 20106	<i>Gnathotitan berkeyi</i> Part of paratype. Irdin Manha. Amer. Mus. No. 20107
(23) Length incisor alv. to condyle (Lmd)	...	569	815	...
(24) Height condyle to angle (Hmd)	196e.	219	270	...
XII. Index: $Hmd \times 100 \div Lmd$...	38%	33%	...
(25) Depth below middle of m_3 (Hmd)	93	88	220	...
XIII. Index: $Hmd \times 100 \div Lmd$...	15%	26%	...
(26) Diastema, from canine to p_1	17e.	45	83	...
(27) p_1-m_3 length (middle)	252e.	268	355	...
XIV. Index: $(p_1-m_3) \times 100 \div Lmd$...	47%	43%	...
(28) p_1-p_4 length (middle)	96e.	96	120	...
(29) m_1-m_3 length (middle)	154	172	235	...
XV. Index: $(p_1-p_4) \times 100 \div (m_1-m_3)$	62%	55%	51%	...
XVI. Index: $(m_1-m_3) \times 100 \div Lmd$...	30%	28%	...
(30) m_1 length (middle)	38	38	53	...
(31) m_2 length (middle)	47	53	70	...
(32) m_2 width at talonid	29	30	38	...
XVII. Index: m_2 width $\times 100 \div m_2$ length	61%	56%	54%	...
(33) m_3 length (middle)	68	82	109	...
(34) i_1 transverse, at base of crown	...	14.5	...	21
(35) i_2 transverse, at base of crown	...	16	18	21.5
(36) i_3 transverse, at base of crown	...	18	...	21.5
(37) p_2-p_4 length (middle)	72e.	80	101	110

TABLE X.—COMPARATIVE MEASUREMENTS OF *Rhinotitan*

	<i>Ripimantoceras formosus</i> No. 21613	<i>Irdin Manha</i> (Ulan Shireh). Type, Irdin Manha (Ulan Shireh). Amer. Mus. No. 21607	<i>Dolichocephalus angustidens</i> Type, Irdin Manha (Ulan Shireh). Amer. Mus. No. 21607	<i>Rhinotitan kaiseni</i> Paratype, Shara Murun. Amer. Mus. No. 20257	<i>Rhinotitan kaiseni</i> Type, Shara Murun. Amer. Mus. No. 20252	<i>Rhinotitan mongoliensis</i> Neotype, Shara Murun. Amer. Mus. No. 20263	<i>Rhinotitan mongoliensis</i> M ³ not up, Shara Murun. Amer. Mus. No. 20256	<i>Rhinotitan andrewsi</i> Type, Shara Murun. Amer. Mus. No. 20271
(1) Basal length (L) pmx. to condyle	700	710	710	700	660	660	779	779
(2) Transverse zygomata (tr.)	396	333	320e	...	439	439
I. Index: tr. $\times 100 \div L$	56%	47%	48%	...	56%	56%
(3) Cheek teeth length (p ¹ -m ³) middle	249	287e.	287e.	275	251	290	301	301
II. Index: (p ¹ -m ³) $\times 100 \div L$	35%	39%	38%	...	38%	38%
(4) p ¹ -p ⁴ length (middle)	94	110	110	105	102	116	115	115
(5) m ¹ -m ³ length (middle)	157	173	173	173	156	180	183	191
III. Index: (p ¹ -p ⁴) $\times 100 \div (m^1-m^3)$	59%	63%	63%	60%	65%	64%	60%	60%
IV. Index: (m ¹ -m ³) $\times 100 \div L$	22%	24%	23%	...	24%	24%
(6) Diastema, post. urf. canine to p ¹	23.5	24	35
(7) m ³ length (parast. to mts.)	67	74	74	74	71	83	83	83
(8) m ³ width (pr. to mesost.)	57	51	51	63	58	69	68	73
V. Index: m ³ width $\times 100 \div m^3$ length	85%	68%	68%	85%	81%	83%	80%	87%
(9) m ² length (pas. to mts.)	53	66	66	67	58*	72	73	76
(10) m ² width (pr. to ms.)	56	49	49	56	59*	65	56	65
VI. Index: m ² width $\times 100 \div m^2$ length	105%	74%	74%	83%	101%	90%	76%	85%
(11) m ¹ length (pas. to mts.)	38	51	51	51	36*	56	59	54.5
(12) m ¹ width (pr. to ms.)	42	39	39	47.5	43	47	47	52
VII. Index: m ¹ width $\times 100 \div m^1$ length	110%	76%	76%	93%	119%	92%	79%	95%
(13) p ⁴ length	24.5	31	31	32.5	29.5	39	39	41
(14) p ⁴ width	36	35	35	40.5	39	44	44	41.5
VIII. Index: p ⁴ width $\times 100 \div p^4$ length	146%	112%	112%	124%	132%	112%	112%	101%
(15) i ¹ transverse, at base of crown	13	12.5	10.5
(16) i ² transverse, at base of crown	14	17	14	16	16	...
(17) i ³ transverse, at base of crown	17	18	15	21	20	...
(18) Nasals, tip to middle nasal notch	161	160	160	...	214
IX. Index: nasal length $\times 100 \div L$	23%	32%
(19) Width across opp. m ³ at mesost.	194	227	...	259	...	252
X. Index: width (19) $\times 100 \div L$	27%	32%	32%
(20) Width across posttymp. processes	227	223	193	313
XI. Index: width (20) $\times 100 \div L$	32%	31%	29%	40%
(21) Lacrimal tubercle to nasal notch	100	113	113	...	92

* Greatly worn.

TABLE XI.—COMPARATIVE MEASUREMENTS OF *Rhinotitan*

	<i>Protitan? cingulatus</i> Type, Irdin Manha. Amer. Mus. No. 26412	<i>Rhinotitan kaiseni</i> Type, Shara Murun. Amer. Mus. No. 20252	<i>Rhinotitan mongoliensis</i> Shara Murun, Amer. Mus. No. 20273	<i>Rhinotitan mongoliensis</i> [H. F. O. J. Amer. Mus. No. 20272] Shara Murun, "Andrews" Amer. Mus. No. 18653	<i>Rhinotitan mongoliensis</i> Type, Shara Murun. Amer. Mus. No. 21605	<i>Rhinotitan</i> Shara Murun, Amer. Mus. No. 21603	<i>Rhinotitan andrewsi</i> Paratype, Shara Murun. Amer. Mus. No. 20251
(23) Length incisor alveoli to condyle (Lmd)	...	540e.	...	611	610e.	604	...
(24) Height condyle to angle (Hmd)	198	...	288	260	...	231	...
XII. Index: $Hmd \times 100 \div Lmd$	42%	...	38%	...
(25) Depth below middle of m_3 (Hmd)	80	89	133	124	122	110	128
XIII. Index: $Hmd \times 100 \div Lm1$...	16%	...	20%	20%	18%	...
(26) Diastema, from canine to p_1	...	35	...	43	36	35	...
(27) p_1 - m_3 length (middle)	250	288	...	299	307	319	329
XIV. Index: $(p_1-m_3) \times 100 \div Lmd$...	53%	...	48%	50%	52%	...
(28) p_1 - p_4 length (middle)	85	104	...	104	104	110	115
(29) m_1 - m_3 length (middle)	162	181	185	192	201	209	210
XV. Index: $(p_1-p_4) \times 100 \div (m_1-m_3)$	52%	57%	...	54%	51%	52%	54%
XVI. Index: $(m_1-m_3) \times 100 \div Lmd$...	33%	...	31%	32%	34%	...
(30) m_1 length (middle)	38	40	45	44	49	45	49
(31) m_2 length (middle)	48	57	56	57	59	64	62
(32) m_2 width at talonid	31	35	31	33	35	31.5	35
XVII. Index: m_2 width $\times 100 \div m_2$ length	64%	61%	55%	57%	59%	49%	56%
(33) m_3 length (middle)	74	83	80	91	89	93	96
(34) i_1 transverse, at base of crown	16	...
(35) i_2 transverse, at base of crown	...	16	...	18	13.5	16	...
(36) i_3 transverse, at base of crown	...	15	12.5	16	...
(37) p_2 - p_4 length (middle)	74	82	97	89	89	93	96

TABLE XII.—COMPARATIVE MEASUREMENTS OF *Pachytitan*

	<i>Epimantoceras formosus</i> Irdin Manba. Amer. Mus. No. 21613	<i>Protitan grangeri</i> Type, Irdin Manba. Amer. Mus. No. 20103	<i>Pachytitan ajax</i> Type, Amer. Mus. No. 21612	<i>Rhinotitan andrewsi</i> Type, Shara Murun, Amer. Mus. No. 20271
(1) Basal length (L) pmx. to condyle.	700	710	...	779
(2) Transverse zygomata (tr.)	396	455	...	439
I. Index: $\text{tr.} \times 100 \div L$	56%	64%	...	56%
(3) Cheek teeth length (p^1 - m^3) middle	249	253	300e.	301
II. Index: $(p^1$ - $m^3) \times 100 \div L$	35%	35%	...	38%
(4) p^1 - p^4 length (middle)	94	97	113e.	115
(5) m^1 - m^3 length (middle)	157	160	190e.	191
III. Index: $(p^1$ - $p^4) \times 100 \div (m^1$ - $m^3)$	59%	60%	59%	60%
IV. Index: $(m^1$ - $m^3) \times 100 \div L$	22%	22%	...	24%
(6) Diastema, post. surf. canine to p^1	23.5	39	33	27
(7) m^3 length (parast. to mts.)	67	73.5	83e.	83
(8) m^3 width (pr. to mesost.)	57	61	77	73
V. Index: m^3 width $\times 100 \div m^3$ length	85%	82%	96%	87%
(9) m^2 length (pas. to mts.)	53	67.5	77	76
(10) m^2 width (pr. to ms.)	56	54	66	65
VI. Index: m^2 width $\times 100 \div m^2$ length	105%	80%	85%	85%
(11) m^1 length (pas. to mts.)	38	43.5	51	54.5
(12) m^1 width (pr. to ms.)	42	42	53	52
VII. Index: m^1 width $\times 100 \div m^1$ length	110%	96%	103%	95%
(13) p^4 length	24.5	27	41	41
(14) p^4 width	36	33	44	41.5
VIII. Index: p^4 width $\times 100 \div p^4$ length	146%	122%	107%	101%
(15) i^1 transverse, at base of crown	13	12
(16) i^2 transverse, at base of crown	14	14.5	13	16
(17) i^3 transverse, at base of crown	17	18.5	16	20
(18) Nasals, tip to middle of nasal notch	161	161	233e.	...
IX. Index: nasal length $\times 100 \div L$	23%	22%
(19) Width across opp. m^3 at mesost.	194	200	...	252
X. Index: width (19) $\times 100 \div L$	27%	28%	...	32%
(20) Width across posttyp. processes	227	256	...	313
XI. Index: width (20) $\times 100 \div L$	32%	36%	...	40%
(21) Lacrimal tubercle to nasal notch	100	130
(22) Height of horn above nasal notch	192	...

TABLE XIII.—COMPARATIVE MEASUREMENTS OF *Parabrontops* AND *Metatitan*

	<i>Parabrontops goblenis</i> Ref. Ulan Gochu. Amer. Mus. No. 26020	<i>Parabrontops goblenis</i> Type. Ardyn Obo. Amer. Mus. No. 20354	<i>Metatitan primus</i> Type. Ulan Shireh. Amer. Mus. No. 26101	<i>Metatitan relictus</i> Type. Houldjin. Amer. Mus. No. 26391	<i>Metatitan relictus</i> Houldjin. Amer. Mus. No. 26397	<i>Metatitan relictus</i> Houldjin. Amer. Mus. No. 26395	<i>Metatitan relictus</i> Houldjin. Amer. Mus. No. 26406	<i>Metatitan relictus</i> Houldjin. Amer. Mus. No. 26399	<i>Metatitan relictus</i> Houldjin. Amer. Mus. No. 26398
(1) Basal length (L) pmx. to condyle	...	576e.	680e.	628	640	670	...	740	778
I. Index: $tr. \times 100 \div L$...	424e.	...	456	461	490	520
(2) Transverse zygomatica (tr.)	...	74%	...	72%	72%	73%	66%
(3) Cheek teeth length (p^1-m^3) middle	268	288e.	298	269	258	273	...	281	318
II. Index: (p^1-m^3) $\times 100 \div L$...	50%	43%	42%	40%	40%	...	37%	40%
(4) p^1-p^4 length (middle)	107	...	110	99	79	96	...	108	118
(5) m^1-m^3 length (middle)	165	180	190	173	174	184	...	172	202
III. Index: (p^1-p^4) $\times 100 \div (m^1-m^3)$	64%	...	57%	57%	45%	52%	...	62%	58%
IV. Index: (m^1-m^3) $\times 100 \div L$...	31%	27%	27%	27%	27%	...	23%	25%
(6) Diastema, post. canine	18	...	0	0	0	0	...	0	0
(7) m^3 length (parast. to mts.)	70	81	86	82	83	79	...	83	89
(8) m^3 width (pr. to mesost.)	60	71	69	62	71	76	...	66	75
V. Index: m^3 width $\times 100 \div m^3$ length	85%	87%	80%	75%	85%	97%	...	79%	84%
(9) m^2 length (pas. to mts.)	62	...	73	62	77	73	...	70	78
(10) m^2 width (pr. to ms.)	55	...	63	57	65	65	...	64	75
VI. Index: m^2 width $\times 100 \div m^2$ length	88%	...	86%	92%	83%	89%	...	91%	95%
(11) m^1 length (pas. to mts.)	45	...	49	42	...	51	...	43	52.5
(12) m^1 width (pr. to ms.)	44	...	54	48	...	65	...	52	58
VII. Index: m^1 width $\times 100 \div m^1$ length	97%	...	110%	114%	...	127%	...	120%	110%
(13) p^4 length	34	35e.	35	34	31	34	34
(14) p^4 width	39	47e.	44	36	40	50.5
VIII. Index: p^4 width $\times 100 \div p^4$ length	114%	134%	125%	105%	117%	107%	148%
(15) i^1 transverse, at base of crown	7	6	7
(16) i^2 transverse, at base of crown	7	6	7	7.5
(17) i^3 transverse, at base of crown	13	10.5	12	14
(18) Nasals, tip to middle nasal notch	130	156e.	151	110	...	165	...	175	...
IX. Index: nasal length $\times 100 \div L$...	27%	22%	17%	...	24%	...	23%	...
(19) Width across opp. m^3 at mesost.	218	256	238	239
X. Index: width (19) $\times 100 \div L$	34%	40%	35%	30%
(20) Width across postymp. processes	...	230	...	357	371	408	399
XI. Index: width (20) $\times 100 \div L$...	39%	...	56%	57%	60%	51%
(22) Height horn above nasal notch	165	...	92	61	...	69	...
			386						

TABLE XIV.—COMPARATIVE MEASUREMENTS OF LOWER JAWS OF *Parabrontops*, *Metatitan* AND *Titanodectes*

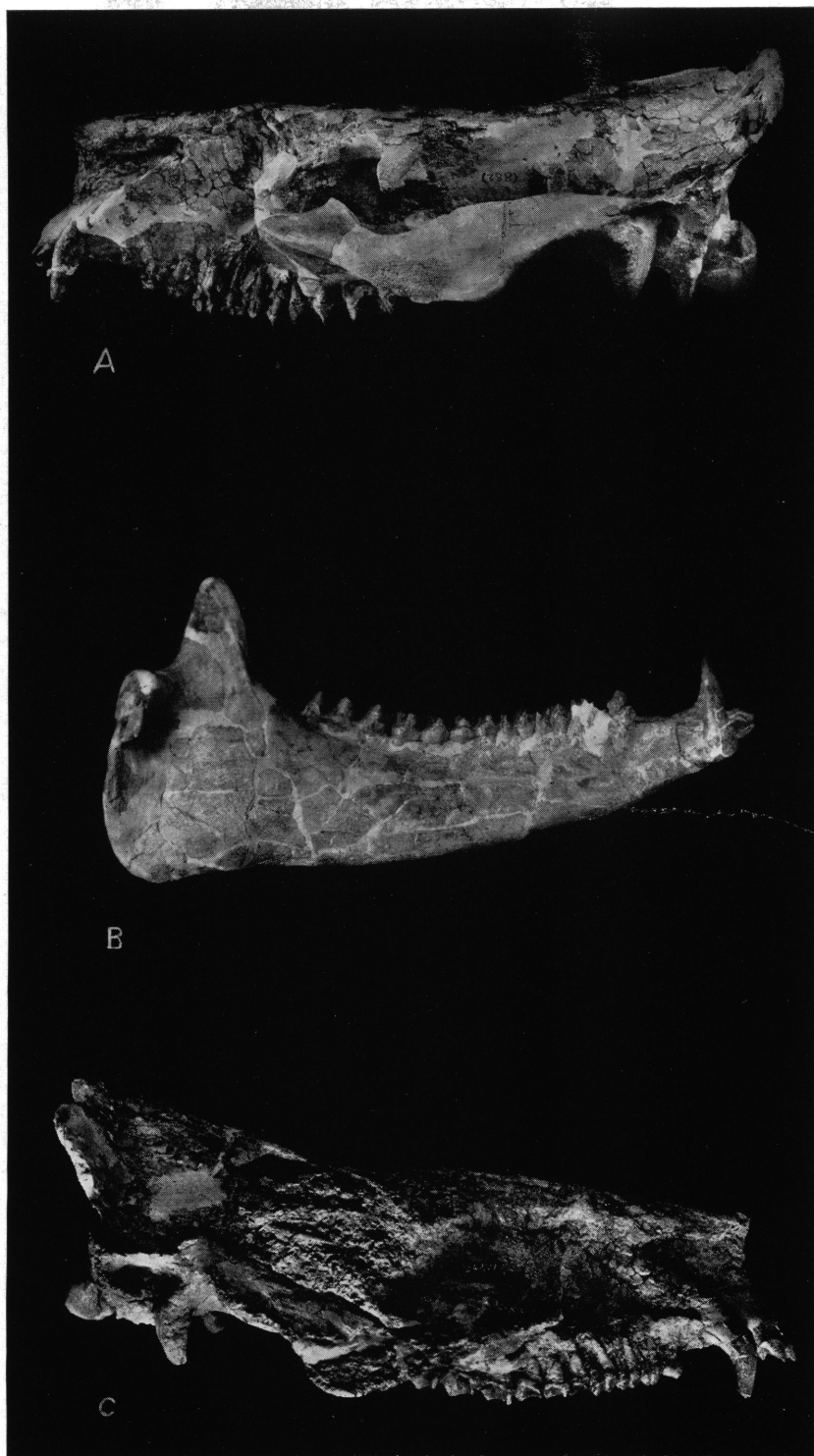
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TABLE XV.—COMPARATIVE MEASUREMENTS OF *Embolotherium*

	<i>Embolotherium andreusi</i> Amer. Mus. No. 26010	<i>Embolotherium andreusi</i> Ulan Gochu. Amer. Mus. No. 26009	<i>Embolotherium andreusi</i> Ulan Gochu. Amer. Mus. No. 26004	<i>Embolotherium ultimum</i> Houldin. Amer. Mus. No. 21604	<i>Embolotherium grangeri</i> Type, Ulan Gochu Amer. Mus. No. 26002
(1) Basal length (L) pmx. to condyle	670cr	730	840	...	750
(2) Transverse zygomata (tr.)	510	505	643	656	592
I. Index: $\text{tr.} \times 100 \div L$...	69%	76%
(3) Cheek teeth length (p^1 - m^3) middle	300	322	329	...	299
II. Index: $(p^1-m^3) \times 100 \div L$	44%	44%	39%
(4) p^1 - p^4 length (middle)	106	118	118	...	104
(5) m^1 - m^3 length (middle)	207	210	225	...	200
III. Index: $(p^1-p^4) \times 100 \div (m^1-m^3)$	51%	56%	52%
IV. Index: $(m^1-m^3) \times 100 \div L$	31%	28%	26%
(6) Diastema, post. surf. canine to p^1	10	11	50	...	32.5
(7) m^3 length (parast. to mts.)	95	94	101	108	93
(8) m^3 width (pr. to mesost.)	79	81	82	97	77
V. Index: m^3 width $\times 100 \div m^3$ length	83%	86%	81%	89%	...
(9) m^2 length (pas. to mts.)	82	72	89	75?	84.5
(10) m^2 width (pr. to ms.)	75	82	77	...	72
VI. Index: m^2 width $\times 100 \div m^2$ length	91%	113%	86%
(11) m^1 length (pas. to mts.)	56	55	63	...	58
(12) m^1 width (pr. to ms.)	58	62	64	...	59
VII. Index: m^1 width $\times 100 \div m^1$ length	103%	112%	101%
(13) p^4 length	40	42	41	...	36
(14) p^4 width	44	51	48	...	43.5
VIII. Index: p^4 width $\times 100 \div p^4$ length	110%	121%	117%
(15) i^1 transverse, at base of crown	...	9
(16) i^2 transverse, at base of crown	...	9.5	16
(17) i^3 transverse, at base of crown	9	8.5	14
(18) Nasals, tip to middle of nasal notch	...	360	330
IX. Index: nasal length $\times 100 \div L$...	49%
(19) Width across opp. m^3 at mesost.	318	248	295	...	278
X. Index: width (19) $\times 100 \div L$	47%	33%	35%
(20) Width across posttym. processes	299	297	299	403	279
XI. Index: width (20) $\times 100 \div L$	44%	40%	35%
(21) Lacrimal tubercle to nasal notch	105

TABLE XVI.—COMPARATIVE MEASUREMENTS OF *Embolotherium*

	<i>Embolotherium andrewsi</i> Goes with mounted skull. Ulan Gochu. Amer. Mus. No. 26009	<i>Embolotherium andrewsi</i> Ulan Gochu. Amer. Mus. No. 26011	<i>Embolotherium andrewsi</i> "Top of Shara Murun." Amer. Mus. No. 21600	<i>Embolotherium andrewsi</i> Ref. Amer. Mus. No. 26006	<i>Embolotherium</i> sp. Amer. Mus. No. 26008
(23) Length incisor alveoli to condyle (Lmd)	595	...	613	659	685e.
(24) Height condyle to angle (Hmd)	260	...	235	270	238
XII. Index: $Hmd \times 100 \div Lmd$	43%	...	38%	41%	34%
(25) Depth below middle of m_3 (Hmd)	121	...	98	178	106
XIII. Index: $Hmd \times 100 \div Lmd$	20%	...	15%	27%	15%
(26) Diastema, from canine to p_1	7	1	...
(27) p_1-m_3 length (middle)	343	...	328e.	390	423
XIV. Index: $(p_1-m_3) \times 100 \div Lmd$	57%	...	49%	59%	61%
(28) p_1-p_4 length (middle)	110	118	122
(29) m_1-m_3 length (middle)	238	243	225	272	283
XV. Index: $(p_1-p_4) \times 100 \div (m_1-m_3)$	46%	43%	43%
XVI. Index: $(m_1-m_3) \times 100 \div Lmd$	40%	...	36%	41%	41%
(30) m_1 length (middle)	52.5	55	46	59	65
(31) m_2 length (middle)	73	75	70	79	84
(32) m_2 width at talonid	46	43	44	44.5	45
XVII. Index: $m_2 \text{ width} \times 100 \div m_2 \text{ length}$	63%	58%	63%	56%	53%
(33) m_3 length (middle)	110	110.5	115	129	132
(34) i_1 transverse, at base of crown	14	...	10
(35) i_2 transverse, at base of crown	12.5	...	15
(36) i_3 transverse, at base of crown	9	...	17
(37) p_2-p_4 length (middle)	93	...	88	116	111



A, B, C, *Metatelmatherium cristatum*, type, Amer. Mus. No. 28411, $\times \frac{1}{6}$.



A, B, *Metatelmatherium cristatum*, type, Amer. Mus. No. 26411, $\times \frac{1}{6}$. C, D, *Metatelmatherium parvum*, type, Amer. Mus. No. 20168, $\times \frac{2}{3}$. E, F, *Desmatotitan tukhumensis*, type, Amer. Mus. No. 21606, $\times \frac{1}{6}$.



A, B, *Hyotitan thomsoni*, type, Amer. Mus. No. 26401, $\times \frac{1}{6}$. C, D, *Protitan grangeri*, type, Amer. Mus. No. 20103, $\times \frac{1}{6}$.



A, B, C, *Epimanteoceras formosus*, type, Amer. Mus. No. 21613, $\times \frac{1}{6}$.



A, B, *Protitan grangeri*, type, Amer. Mus. No. 20103, $\times \frac{1}{6}$.



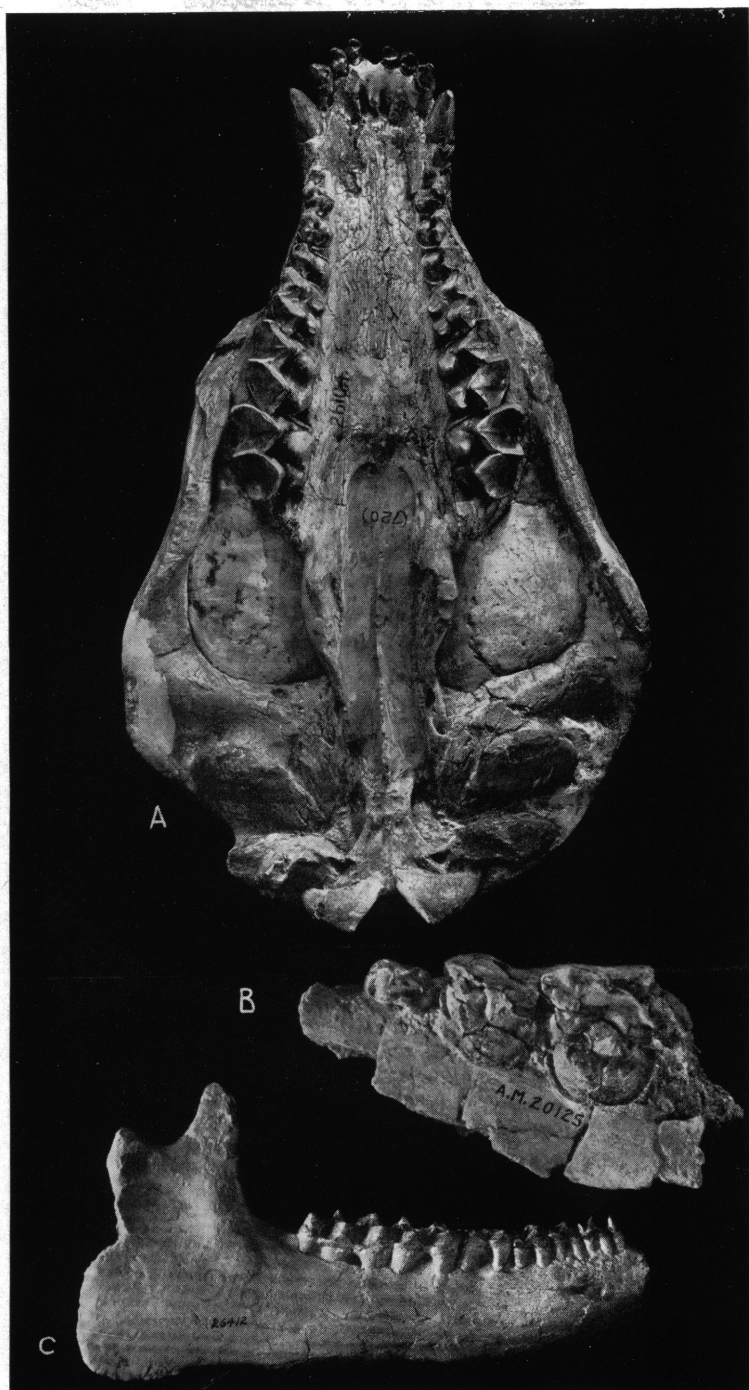
Protitan grangeri, type, Amer. Mus. No. 20103, $\times \frac{1}{6}$.



A, B, C, *Protitan minor*, type, Amer. Mus. No. 26416, $\times \frac{1}{6}$.



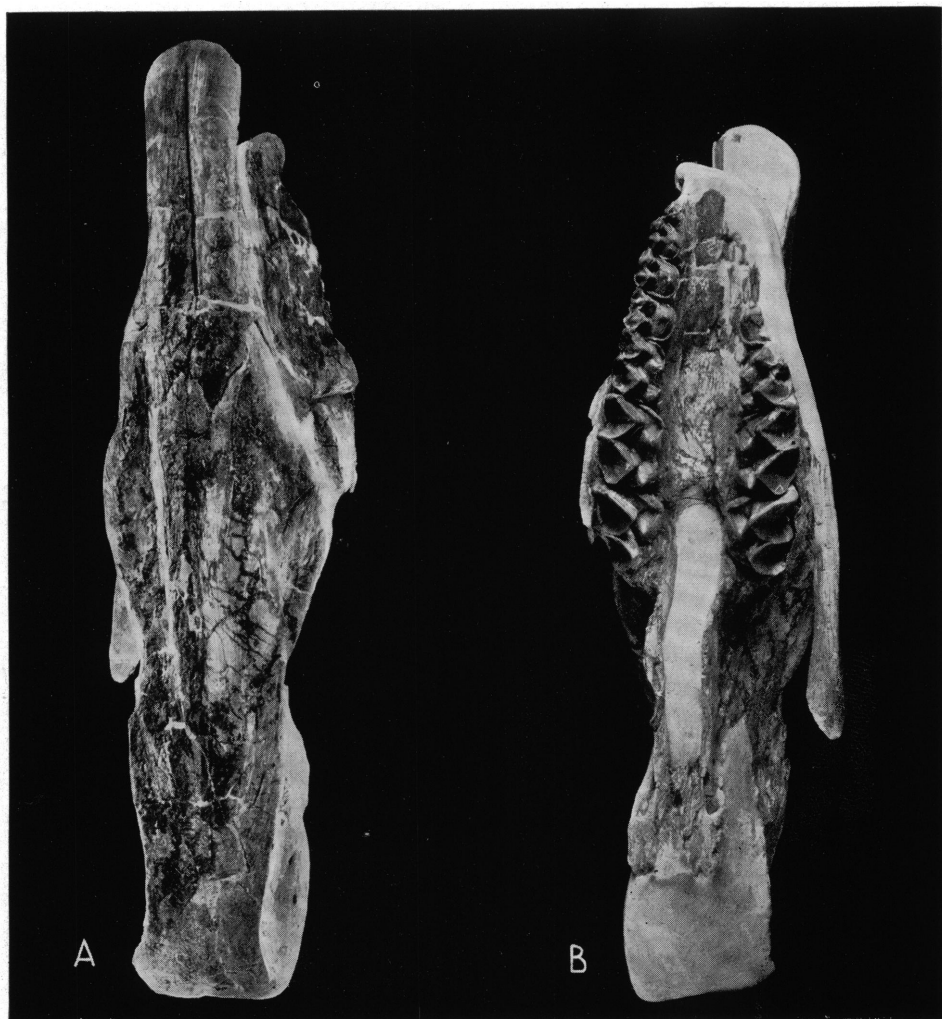
A, B, *Protitan robustus*, type, Amer. Mus. No. 20104, $\times \frac{1}{6}$. C, D, *Protitan robustus*, doubtfully referred lower jaw, Amer. Mus. No. 20110, $\times \frac{1}{6}$. E, *Protitan? cingulatus*, type, Amer. Mus. No. 26412, $\times \frac{1}{6}$.



A, *Protitan bellus*, type, Amer. Mus. No. 26104, $\times \frac{1}{4}$. B, *Protitan obliquidens*, type, Amer. Mus. No. 20125, $\times \frac{2}{3}$. C, *Protitan? cingulatus*, type, Amer. Mus. No. 26412, $\times \frac{1}{6}$.



A, B, *Microtitan mongoliensis*, neotype, Amer. Mus. No. 22099, $\times \frac{2}{3}$. C, *Microtitan mongoliensis*, Amer. Mus. No. 21611, referred maxilla, $\times \frac{2}{3}$.



A, B, *Dolichorhinoides angustidens*, type, Amer. Mus. No. 21607, $\times \frac{1}{6}$.



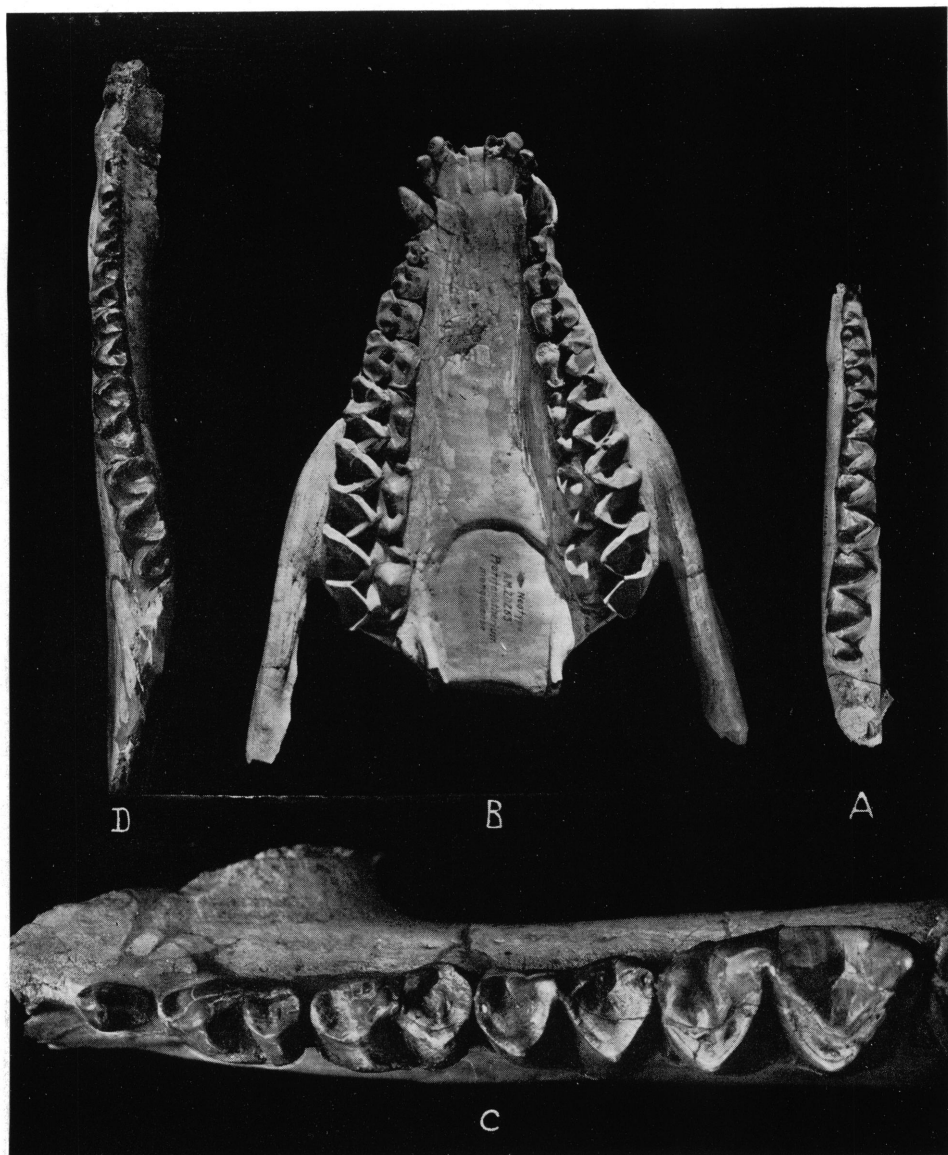
A, B, *Dolichorhinoides angustidens*, type, Amer. Mus. No. 21607, $\times \frac{1}{6}$.



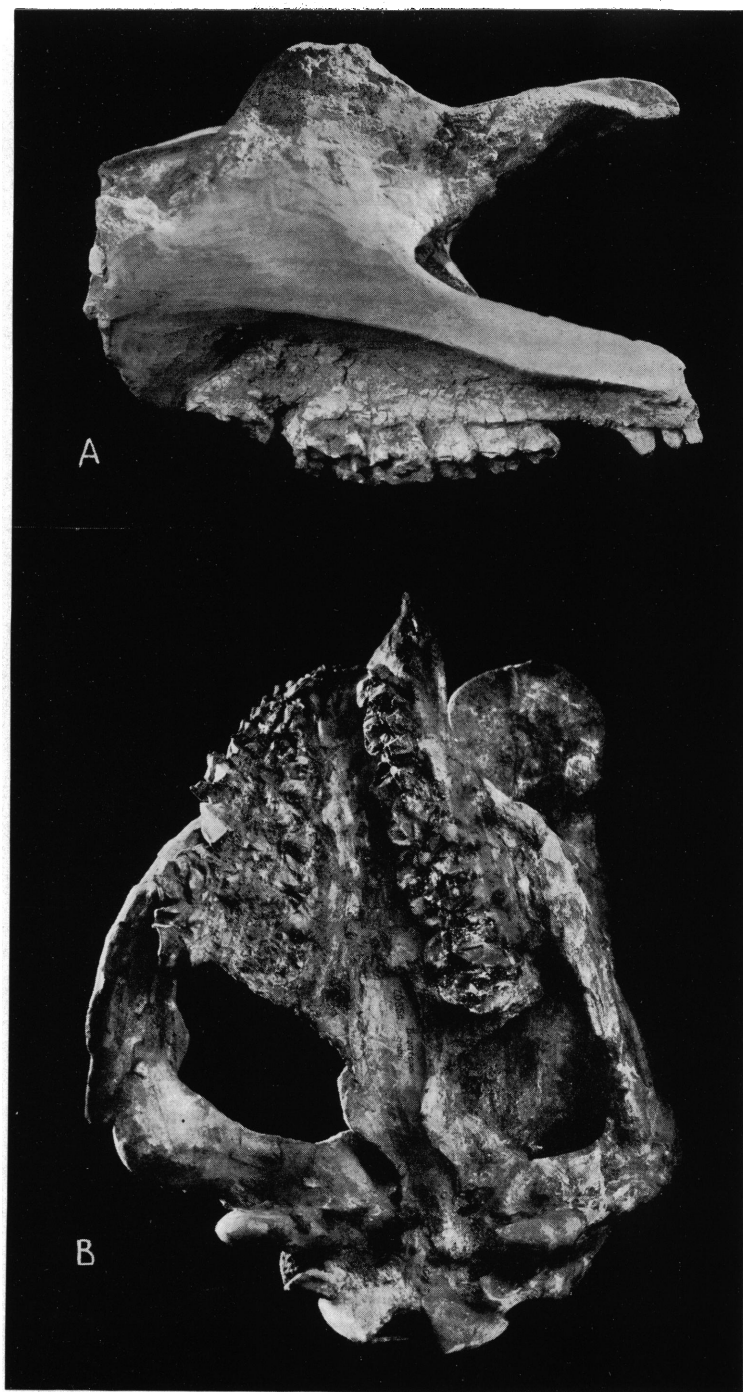
A, B, C, *Gnathotitan berkeyi*, type, Amer. Mus. No. 20106, circa $\times \frac{1}{6}$.



A, B, C, *Rhinotitan kaiseni*, type, Amer. Mus. No. 20252, $\times \frac{1}{6}$.



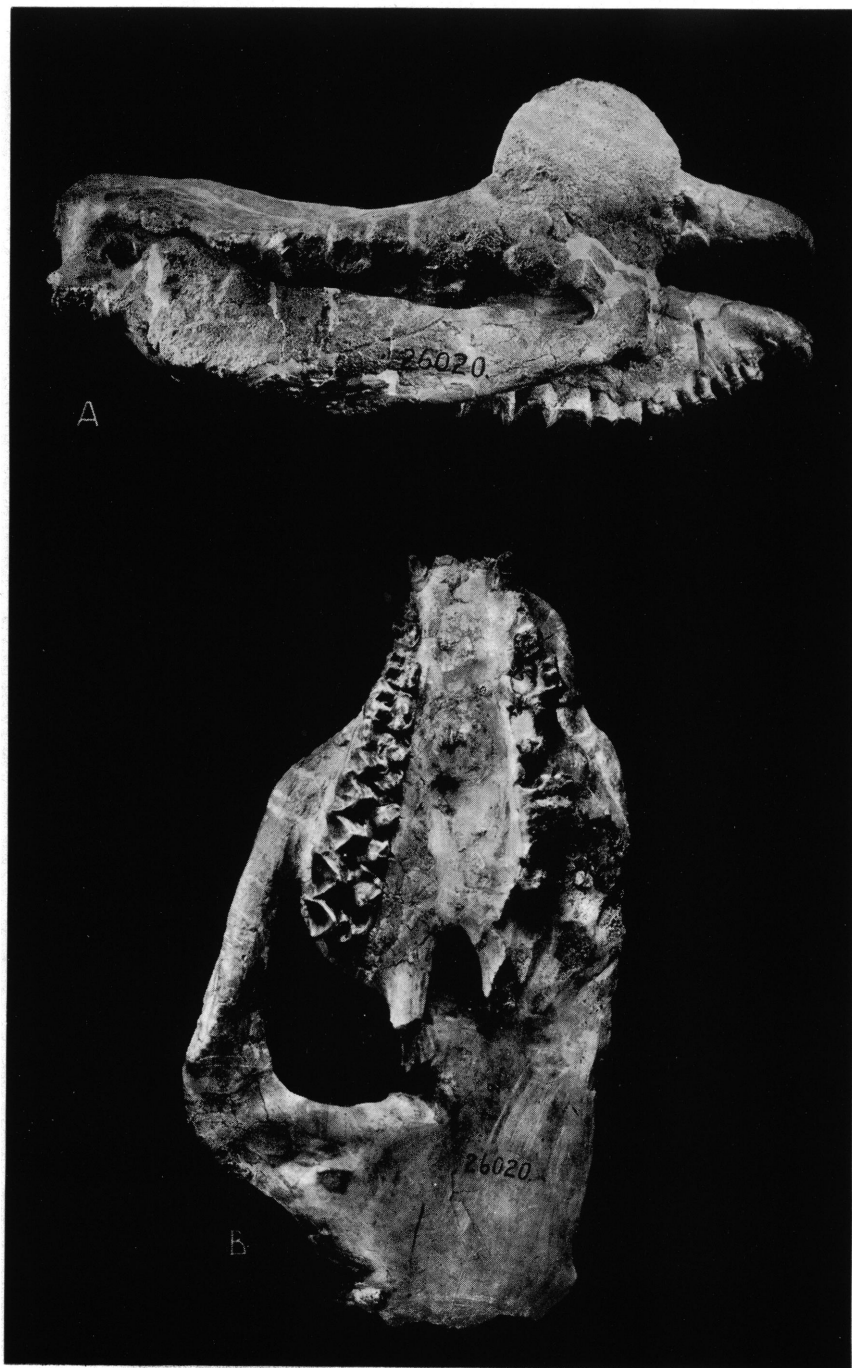
A, *Rhinotitan mongoliensis*, type, Amer. Mus. No. 18653, $\times \frac{1}{6}$. B, *Rhinotitan mongoliensis*, Amer. Mus. No. 20263, $\times \frac{1}{6}$. C, *Rhinotitan mongoliensis*, Amer. Mus. No. 20256, $\times \frac{2}{3}$. D, *Rhinotitan andrewsi*, Amer. Mus. No. 20251, $\times \frac{1}{6}$.



A, *Pachytitan ajax*, type, Amer. Mus. No. 21612, $\times \frac{1}{6}$. B, *Parabrontos gobiensis*, type, Amer. Mus. No. 20354, $\times \frac{1}{6}$.



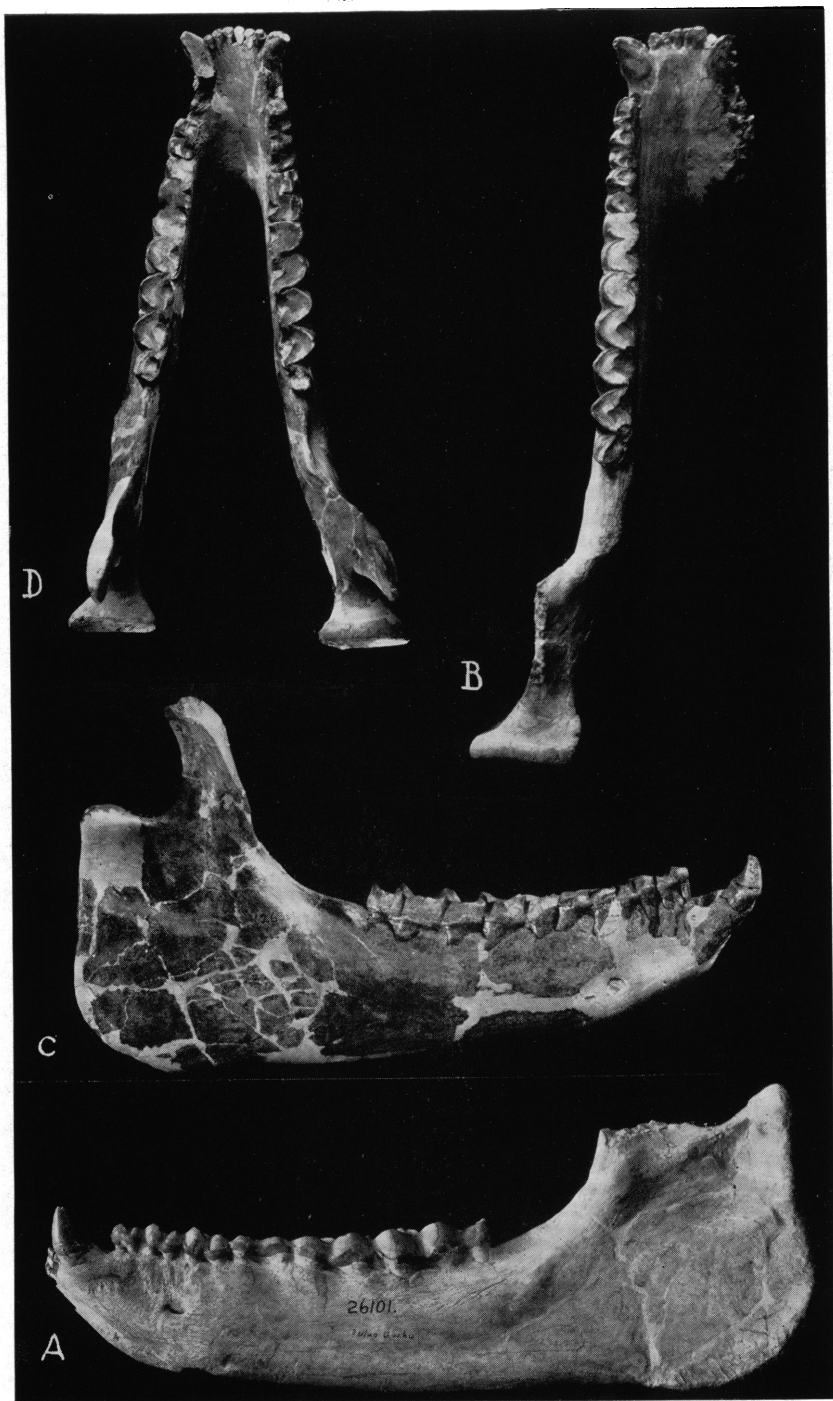
A, B, *Parabrontops gobiensis*, type, Amer. Mus. No. 20354, $\times \frac{1}{4}$.



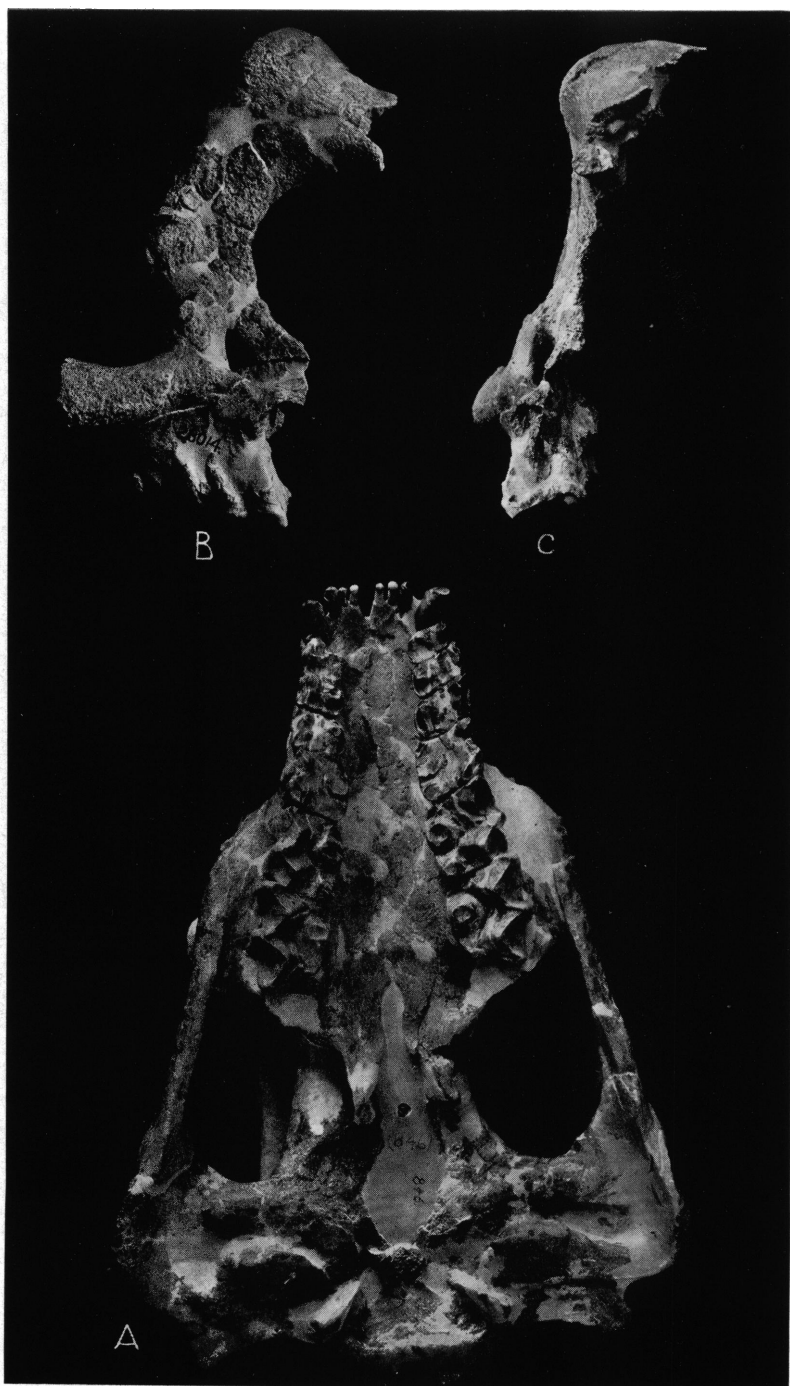
A, B, *Parabrontops gobiensis*, Amer. Mus. No. 26020. $\times \frac{1}{4}$.



A, B, C, *Metatitan primus*, type, Amer. Mus. No. 26101, A, B, $\times \frac{1}{6}$; C, $\times \frac{1}{3}$.



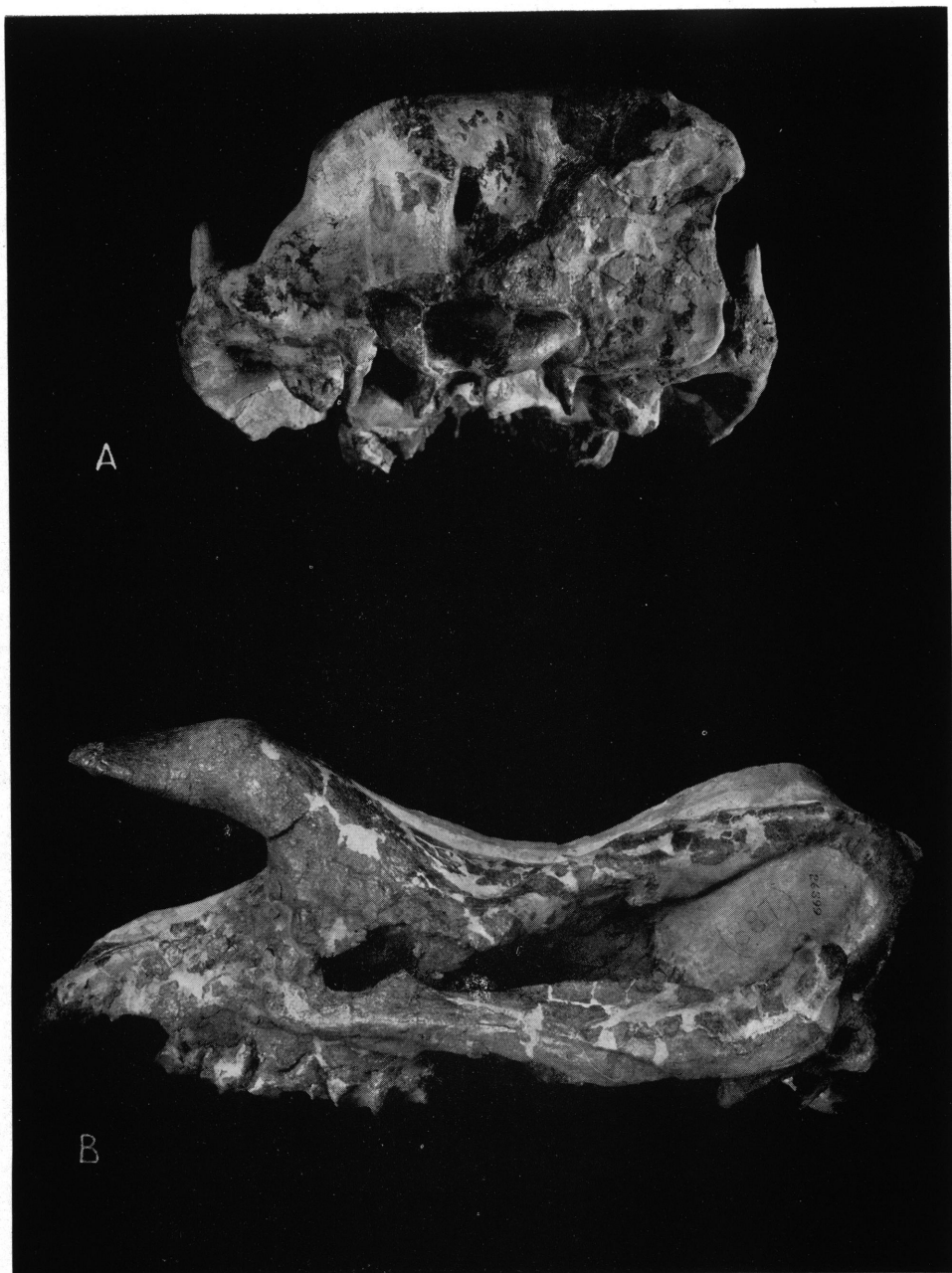
A, B, *Metatitan primus*, type, Amer. Mus. No. 26101, $\times \frac{1}{6}$. C, D, *Metatitan relictus*, type, Amer. Mus. No. 26391, $\times \frac{1}{6}$.



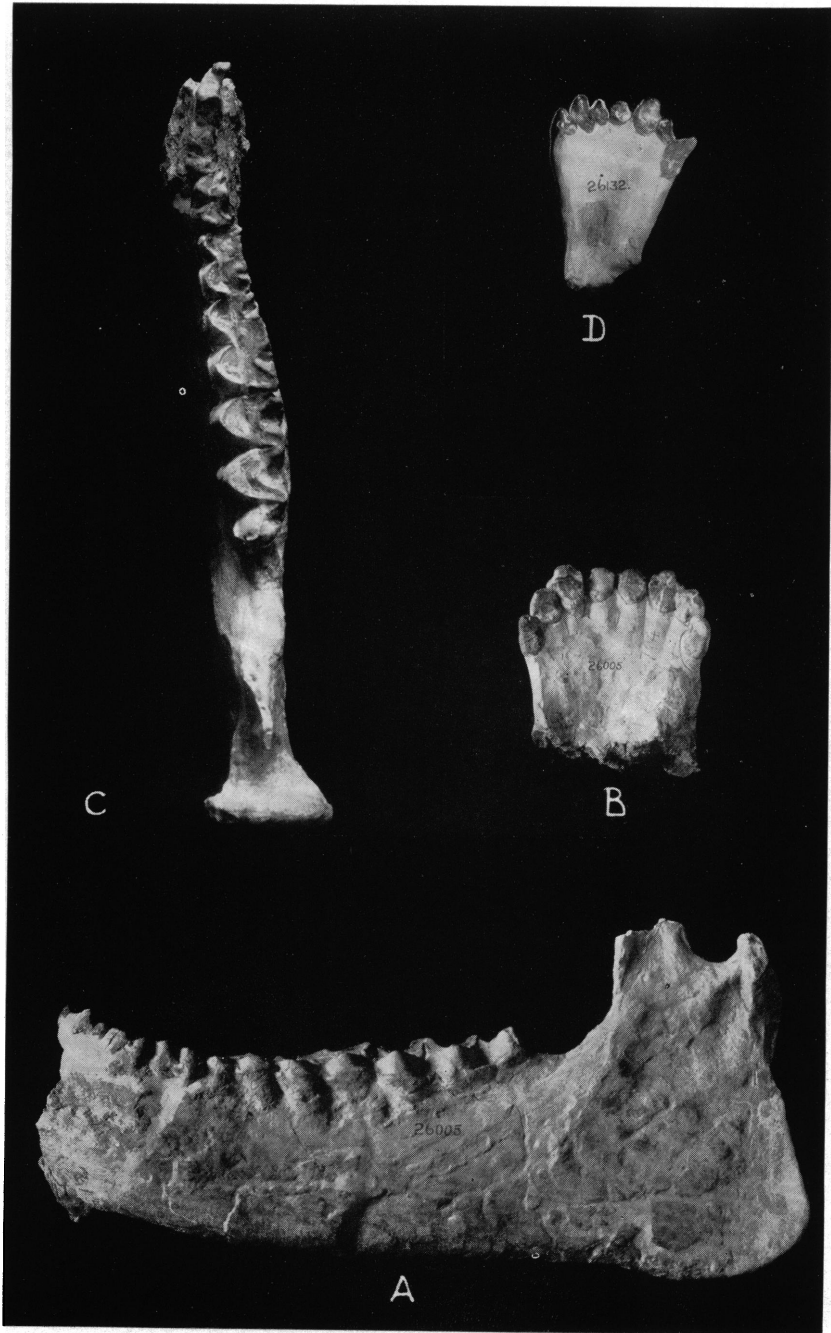
A, *Metatitan relictus*, type, Amer. Mus. No. 26391, $\times \frac{1}{6}$. B, C, *Metatitan progressus*, type, Amer. Mus. No. 26014, $\times \frac{1}{6}$.



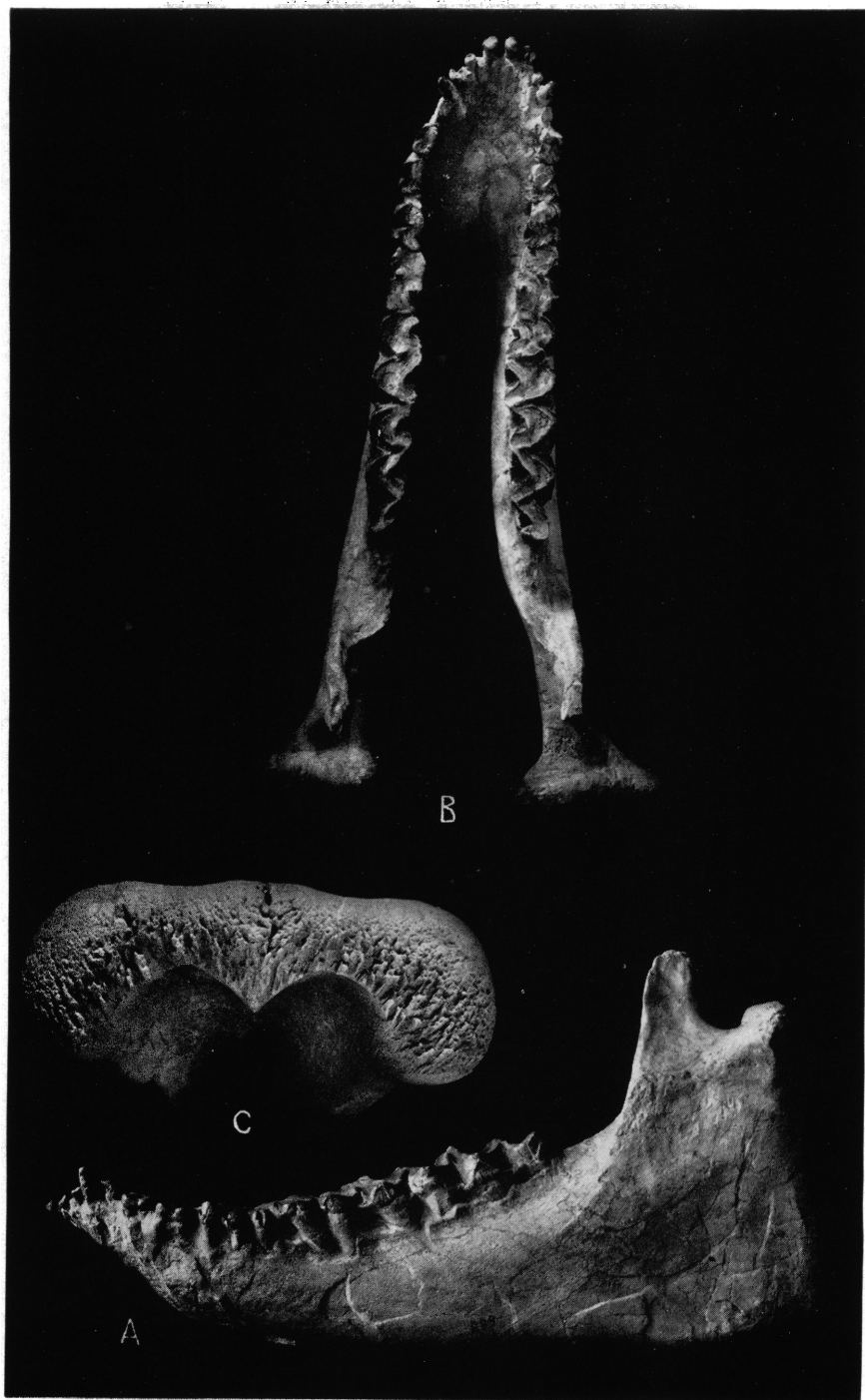
Metatitan relictus, Amer. Mus. No. 26398, $\times \frac{1}{6}$.



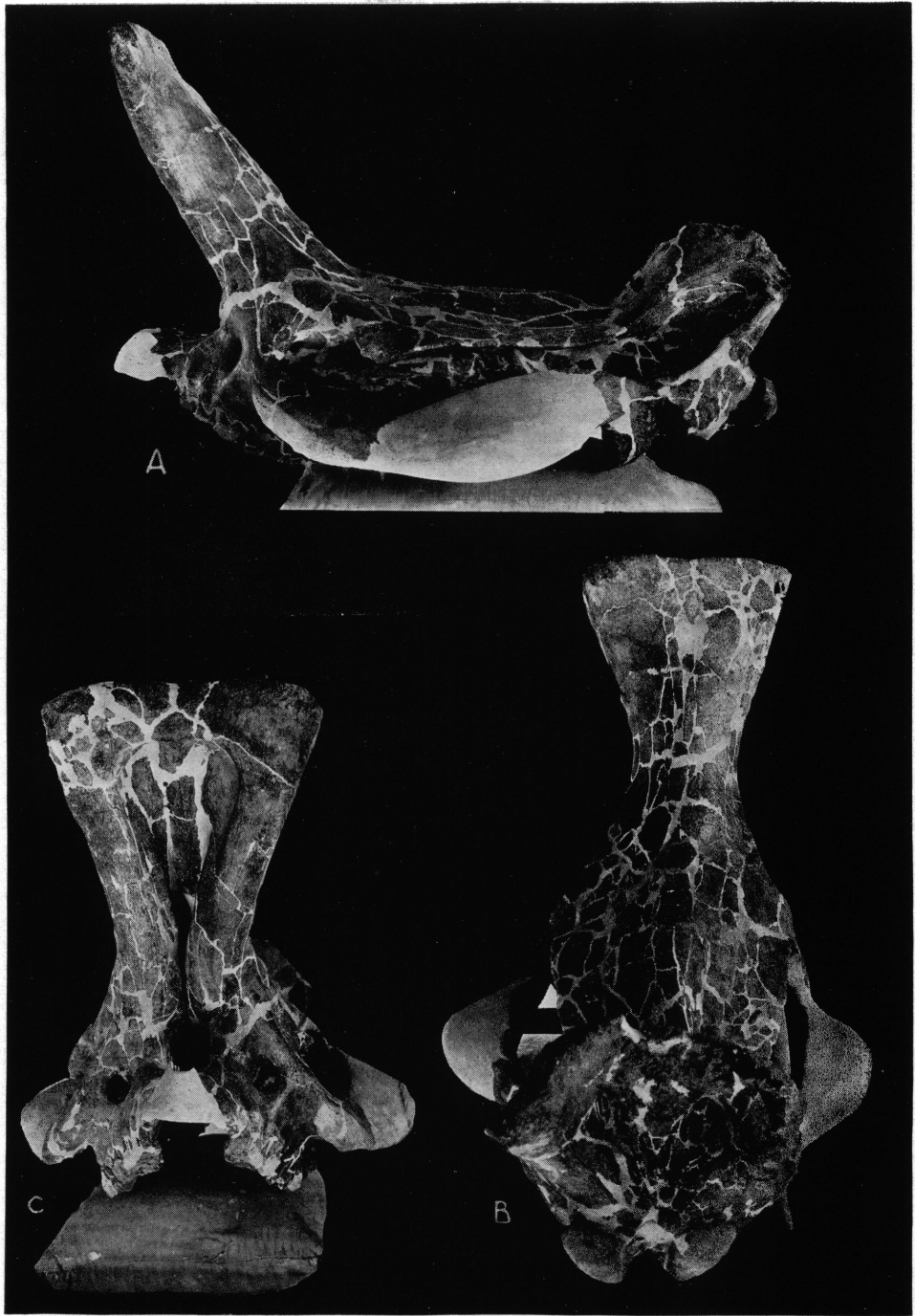
A, *Metatitan relictus*, Amer. Mus. No. 26397, $\times \frac{1}{6}$. B, *Metatitan relictus*, Amer. Mus. No. 26399, $\times \frac{1}{6}$.



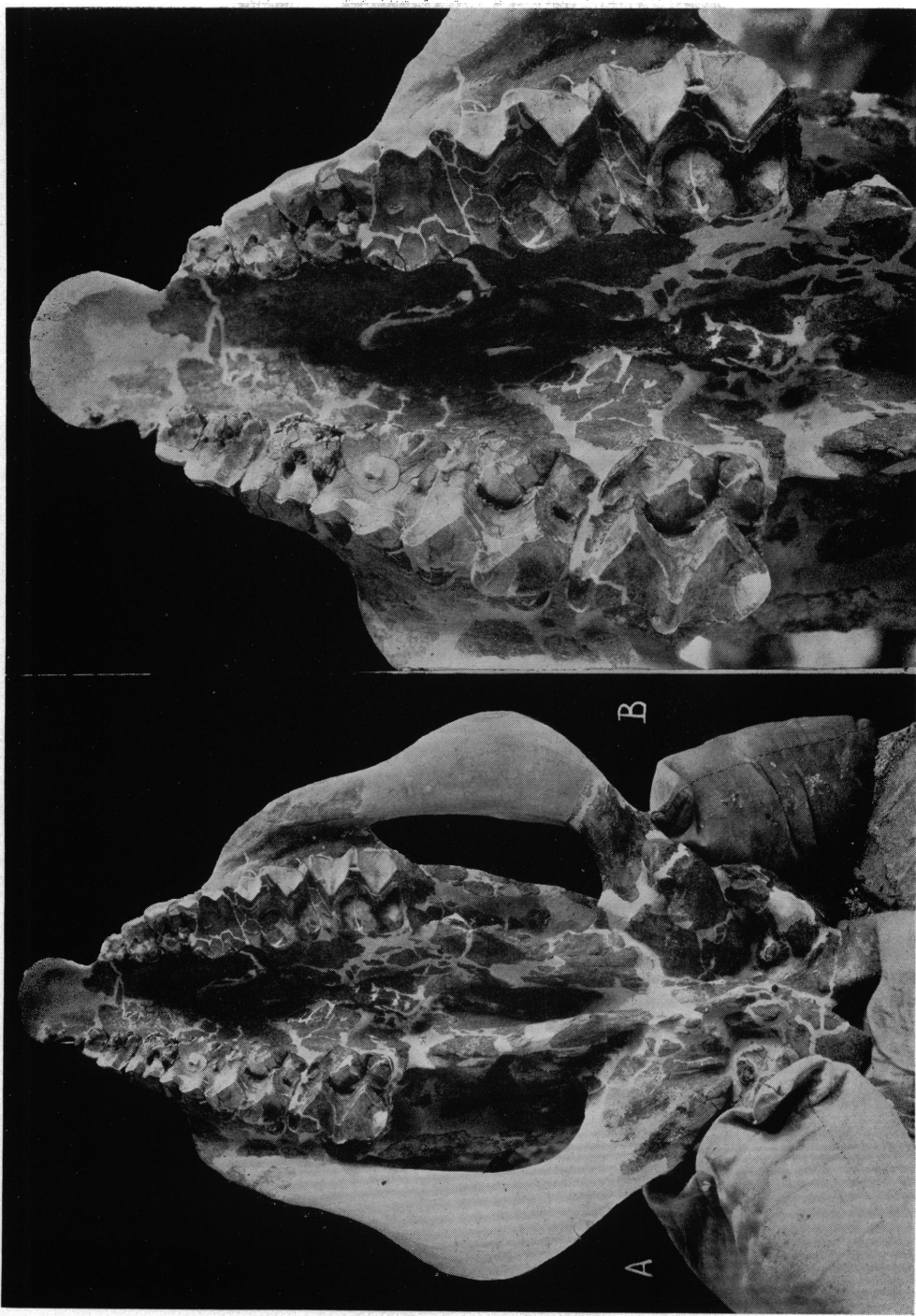
A, B, C, *Titanodectes ingens*, type, Amer. Mus. No. 26005, $\times \frac{1}{4}$. D, *Titanodectes minor*, part of type jaw, Amer. Mus. No. 26132, $\times \frac{1}{6}$.



A, B, *Embolotherium andrewsi*, Amer. Mus. No. 26009, $\times \frac{1}{6}$. C, *Embolotherium andrewsi*, Amer. Mus. No. 26004, scale unknown.



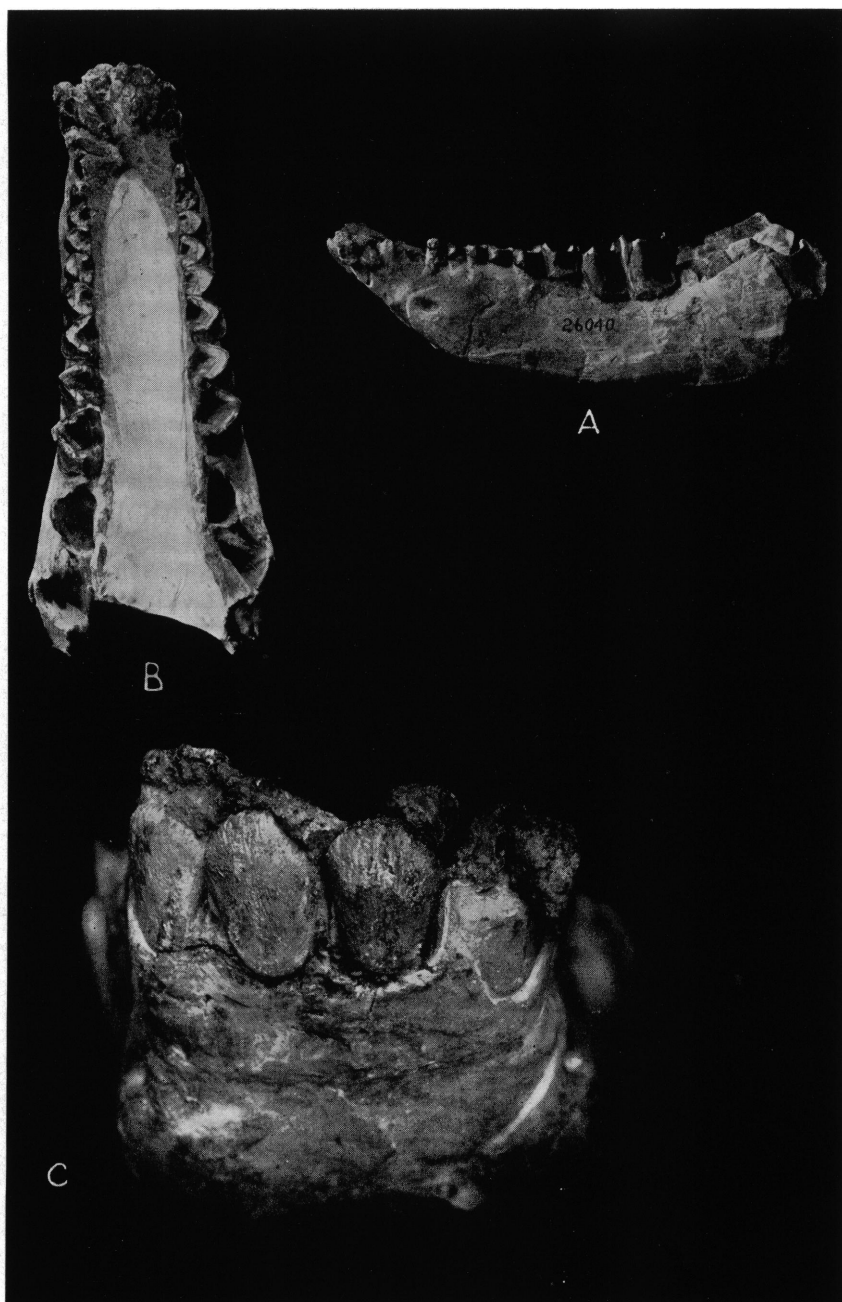
A, B, C, *Embolotherium andrewsi*, Amer. Mus. No. 26000, scale unknown.



A, B, *Embolotherium andreus*, Amer. Mus. No. 26000, scale unknown.



Embolotherium andrewsi, Amer. Mus. No. 26010, $\times \frac{1}{6}$.



A, B, C, *Embolotherium loucksii*, Amer. Mus. No. 26040, A, B, *circa* $\times \frac{1}{6}$; C, $\times \frac{2}{3}$.



Embolotherium ultimum, type, Amer. Mus. No. 21604, $\times \frac{1}{6}$

