

**Article VIII.—THE FOUR PHYLA OF OLIGOCENE
TITANOTHERES.¹**

TITANOTHERE CONTRIBUTIONS, No. 4.²

By HENRY FAIRFIELD OSBORN.

My first review of this group, entitled 'Cranial Evolution of Titanotherium' (Titanotherium Contributions No. 3), was based upon examination of only part of the original material; it included a preliminary revision of the species by the distinction of growth, sexual and variable characters, and by the method of sections of different parts of the skull.

Two errors invalidated this review. First, the stratigraphical or geological sequence of the types examined was not fully known, and, second, as a consequence, the group was treated as more or less monophyletic with certain side branches.

This second review is an abstract of a portion of the results obtained for the U. S. Geological Survey monograph, 'The Titanotheres,' now in preparation. It covers practically all the type material in the Yale, National, American, and Harvard Museums, and advantage has been taken of the invaluable field observations by Hatcher of the levels on which the different skulls in the National Museum collection were discovered. The section method also has been very greatly extended and, taken in connection with the teeth and the detailed structure of the skull, has proved to be a sure criterion of specific and phyletic character.

Beginning in January, 1901, the work for the monograph advanced uninfluenced by any theory as to the evolution of these mammals until finally, in July, all the data were put together with most interesting results, which may be briefly summarized as follows:

¹ The late Professor O. C. Marsh of Yale University devoted many years to the collection of materials and preparation of plates and figures for a monograph on the group treated in this paper. He also completed several valuable papers, but left no manuscript. Full acknowledgment of this important service to palæontology will be made by the writer in the final treatise.

² See contributions 1-3 in Bibliography.

I. THE ADAPTIVE RADIATION.

The Oligocene Titanotheres consisted of at least four contemporary phyla, to which the prior generic names *Titanotherium*, *Megacerops*, *Symborodon*, and *Brontotherium* may be applied.

They represent an adaptive radiation for different local habitat, different modes of feeding, fighting, locomotion, etc., which took origin, in part at least, in the Middle or Upper Eocene. Europe and Asia also may have shared in this radiation, since Titanotheres are now definitely known in the Balkan region.

The main phyletic characters are analogous to those recently (Osborn, 1900, p. 231) determined among Rhinoceroses; the great antiquity of the lines leading to the existing species of Rhinoceroses necessitated the revival of a number of discarded generic names to distinguish them. Similarly the separateness of four of the Titanothera phyla, throughout the Oligocene and possibly from the Eocene, render it desirable to revive certain generic names which in my first review I considered undefinable.

Radiation involved three main sets of characters, two of which were correlated:

First, dolichocephaly and brachycephaly, associated with numerous changes in the skull and teeth, and, in at least two phyla, with longer and shorter limbs.

Second, four distinct types in the shape and position of the horns, correlated with the structure of the nasals and frontals and indicative of different modes of combat among the males.

Third, canines of different form; and, finally, the presence of one or two pairs of functional incisor teeth, or the total degeneration of these teeth.

2. THE FOUR GENERA.

Titanotherium Leidy applies to long-limbed animals with long skulls, persistently long and broad nasals, short triangu-

lar horns placed slightly in front of the eyes, vestigial incisors, $\frac{2-0}{2-0}$, large canine teeth. Known from the base to the summit of the Oligocene.

Megacerops Leidy applies to *Titanotheres* with broad skulls, nasals progressively shortening, short horns rounded or oval in section, shifting anteriorly, one or two pairs of incisor teeth, $\frac{2-1}{2-1}$, medium sized canine teeth. Known from the base to the summit of the Oligocene.

Probably related to this are the subgenera of the types named *Allops* and *Diploclonus* by Marsh, differing from the above in horn characters. Known chiefly from the Upper Beds.

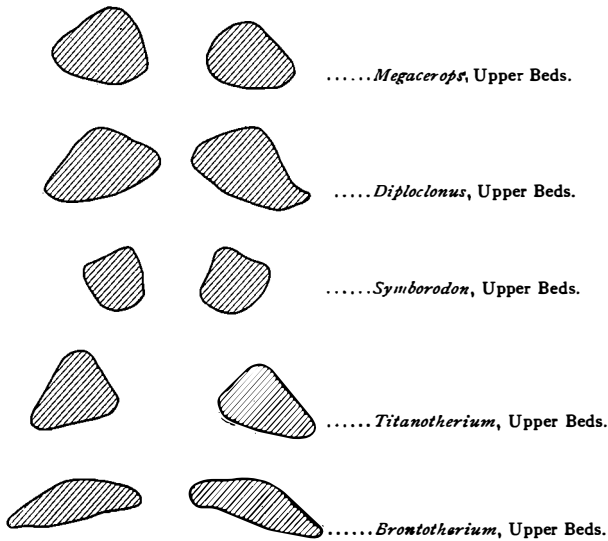


Fig. 1. Characteristic basal horn sections.

Symborodon Cope includes *Titanotheres* with skulls of varying proportion, nasals slender and progressively shortening, horns elongate and peculiar in being placed above the eyes instead of shifting forwards, incisors vestigial $\frac{2-0}{2-0}$, canines small, approximated. Known only from the Middle and Upper Beds.

Brontotherium Marsh embraces the largest Titanotheres, with very broad zygomatic arches, nasals shortening while horns elongate and shift forwards; incisors persistent, $\frac{2}{3}$ in the males, canines stout and obtuse.

Representatives of *Titanotherium* and *Megacerops* can now be continuously traced from the base to the summit of the Oligocene. Primitive species of *Brontotherium* also appear at the base, although the phyletic sequence through the Middle to the Upper Beds is not so clear. *Symborodon* suddenly appears in the Middle Beds.

3. NEWLY OBSERVED PROGRESSIVE CHARACTERS.

In addition to the progressive and retrogressive characters previously recorded by various writers (Osborn, 1896, pp. 162-174), are several of great value in the determination of species. (1) In the complication of the premolar teeth, one or more phyla progress in common, although the rate is unequal; for example, the double internal cones of the upper premolars are precociously developed in *Titanotherium* and very gradually so in *Megacerops*. (2) The cranial and many of the dental characters are profoundly affected by the progressive shortening or lengthening of the skull as recently explained in some detail by the writer (Osborn, 1902). (3) The cingulum around the molar and premolar teeth becomes progressively stronger in *Titanotherium* and *Megacerops*, and progressively weaker in *Symborodon* and *Brontotherium*. (4) The persistence or degeneration of incisor teeth are far more constant systematic characters than appeared to be the case in my first review.

In brief, each genus or phylum has its distinctive, persistent, progressive, and retrogressive characters, of which the above are a few examples out of many.

4. THE SUCCESSION OF SPECIES.

Phylum I.

Dolichocephalic Titanotheres with short, divergent, triquetrous horns placed slightly in advance of the orbits; nasals elon-

gate and square; incisors vestigial; canines very long and pointed; cingulum progressively developing; premolars $\frac{4}{4}$; buccal processes of zygomata deep rather than broad.

GENUS TITANOTHERIUM LEIDY.

The type of the genus is *T. proutii* Leidy, represented by the posterior portion of a jaw fortunately preserved in the National Museum, recorded from the base of the Titanotherium Beds. The genus is further characterized by a comparison of *T. heloceras*, *T. trigonoceras*, and *T. ingens*. It may have taken origin from *Diplacodon elatus* or *D. emarginatus* of the Upper Eocene or Uinta Beds.

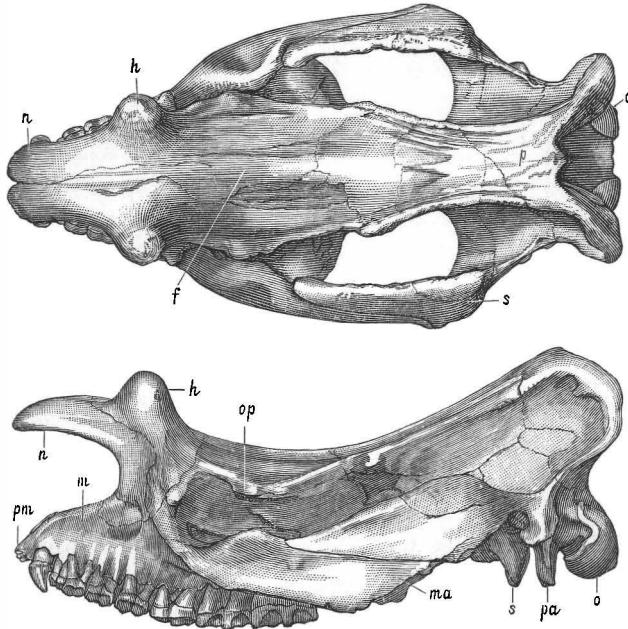


Fig. 2. *Titanotherium heloceras* (Cope). (U. S. Nat. Mus. No. 4260, Sk. Q.) $\times \frac{1}{2}$.

LOWER BEDS.

***T. heloceras* Cope.**—This is probably the earliest and most primitive representative of the long-skulled series. The doubt

arises from the imperfect condition of the type. With this species, however, is probably associated a skull (Nat. Mus. No. 4260) definitely recorded by Hatcher as from the Lower Beds and exhibiting a number of undoubted *Titanotherium* characters.

MIDDLE BEDS.

T. trigonoceras *Cope*.—Animals of middle size with long metapodials, represented by numerous specimens in the American and National Museums, show the state of evolution of this phylum in the Middle Beds. As compared with *T. heloceras* there is a marked progression in size, in the shaping of the horns, the development of the paired premolar cones, and of the cingulum on the grinding teeth.

UPPER BEDS.

T. ingens *Marsh* (Syn., *Menops varians* *Marsh*).—These very large, long-skulled and long-footed Titanotheres, first described by Marsh as *Brontotherium*¹ *ingens*, are definitely recorded by Hatcher from the Upper Beds, and show a corresponding increase in size and in all other progressive characters. The incisors are vestigial, the canines very long and powerful; the cingulum on the grinding teeth is very pronounced in both males and females. There is a marked difference between the sexes in the size of the horns and canines.

Phylum II.

Brachycephalic Titanotheres with short horns shifting forwards, rounded to oval at summits; nasals progressively reduced in length and broadening at the extremities; one or two pairs of persistent incisor teeth, above and below; canines pointed, of medium length; premolars, $\frac{4-4}{4-3}$; zygomata progressively expanding into convex buccal processes; cranium not greatly produced behind zygomata.

¹ As explained below, the name *Brontotherium* applies to the animals called *Titanops* by Marsh.

GENUS MEGACEROPS LEIDY.

This genus may have taken origin in the broad-skulled *Limnohyops manteoceras* or *Palæosyops paludosus* of the Eocene, although no horned type of the latter is known. It is known from the imperfect type of *M. coloradensis* and a very rich variety of species from the Lower, Middle, and Upper Beds, which have previously been referred to other genera. In the typical members the horns are slightly divergent and retroverted. There is a wide variation in progressive character between such species as *M. brachycephalus* and *dispar*, *M. bicornutus*, *M. selwynianus*, *M. tichoceras*, *M. robustus*, but it is found that the variations of age, growth, and sex, especially in species such as *M. dispar* and *M. robustus*, bridge over the differences between the types of said species and present intermediate forms. Furthermore these species are much more closely united to the general type of *Megacerops* than to any other genus.

LOWER BEDS.

***Megacerops brachycephalus*, sp. nov.**

The type of this species is No. 4261, U. S. Nat. Mus. It includes very small, broad-skulled Titanotheres with very rudimentary second internal cones upon the upper premolars; nasals elongate, narrowing anteriorly, as in *Palæosyops*. Horns of anteroposterior

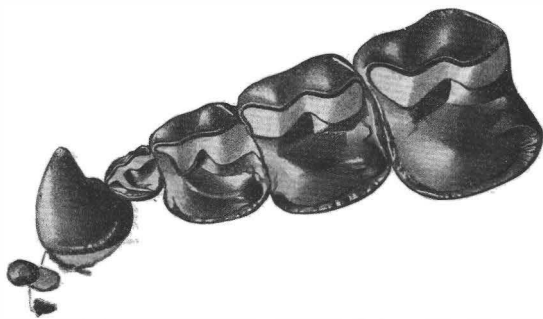


Fig. 3. *Megacerops brachycephalus*. (U. S. Nat. Mus. No. 4258, Sk. F.) Not the type. $\times \frac{1}{2}$.

oval section placed above orbits. It is represented in the National Museum by numerous skulls besides the type, all [February, 1902.]

collected and recorded by Hatcher. One of these skulls was provisionally referred by him to *Teleodus avus*, from which this species is quite distinct.

MIDDLE BEDS.

Megacerops dispar Marsh (Syn., *Brontops validus* Marsh). —Represented by the type, No. 4941, U. S. Nat. Mus., and numerous fine male and female skulls in the National Museum, collected and accurately recorded as to level by

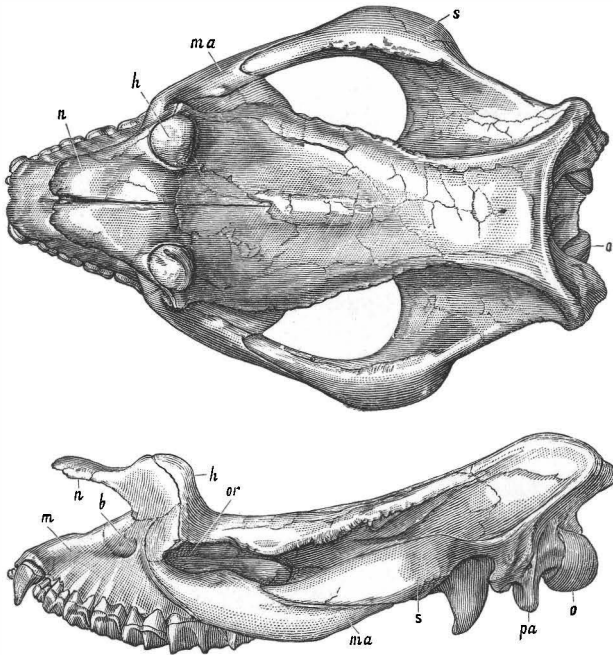


Fig. 4. *Megacerops brachycephalus*. (U. S. Nat. Mus. No. 4258, Sk. F.) Not the type. This skull was figured by Marsh (*Amer. Jour. Sci.*, Oct., 1887) as *Brontops dispar*. $\times \frac{1}{4}$.

Hatcher. The incisors vary from two to one. Canines prominent, pointed. Premolars, $\frac{4-3}{4-3}$, with internal cones more distinct than in *M. brachycephalus*. Nasals shorter; horns longer, broader in section at the base; zygomata more expanded.

LEVEL NOT RECORDED

Megacerops avus Marsh.—This type jaw, distinguished by the presence of three lower incisors, belongs to a much larger animal than *M. brachycephalus*. The presence of an outer lower incisor may be due to reversion or to the retention of a milk tooth; all young Titanotheres have three milk incisors. The formula, I_3, P_3 , does not appear sufficient to remove this type generically, because the form of the canine, shape of the jaw, feeble development of the cingulum, etc., lead to placing it in *Megacerops*.

M. coloradensis Leidy.—Horns of medium length, of relatively slender cylindrical section. Nasals elongate, decurved, and narrow anteriorly. This is the type species.

M. angustigenis Cope.—Type in Ottawa Museum. Horns as in *M. coloradensis*, but nasals abbreviated and expanding anteriorly.

M. ? selwynianus Cope.—Level not recorded, probably Middle Beds. Type in Ottawa Museum. Nasals extremely narrow, elongate, with highly arched inferior surface as in the species next to be described.

MIDDLE BEDS.

Megacerops bicornutus, sp. nov.

Type No. 1476, cotype No. 1081, Amer. Mus. Horns directed anteriorly. Hornlets upon the inner and anterior mid-portion of the horn. Basal section of the horn slightly oval, subtransverse. Nasals narrow and relatively elongate. Sharp malar bridge in front of orbit. Orbit large.

This animal stands nearest *M. selwynianus*, although distinguished by the greater size and slightly greater width of the nasals. The sharp malar bridge is the most absolute character. The two hornlets are possibly variations.

UPPER BEDS.

Megacerops tichoceras Scott & Osborn.—Type skull in Harvard Museum. This is distinguished from *M. dispar* by

the somewhat abbreviated nasals, greater expansion of the buccal processes, and two distinct internal cones upon the superior premolars. It is represented also by a number of

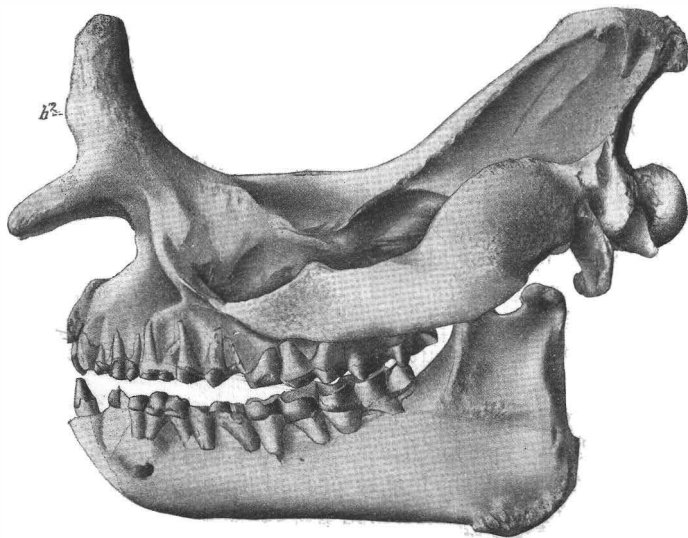


Fig. 5. *Megacerops bicornutus*. (Amer. Mus. Nat. Hist. No. 1476.) Type. $\times \frac{1}{2}$.

large skulls in the National Museum definitely recorded by Hatcher from the Upper Beds.

***Megacerops marshi*, sp. nov.**

Type, Skull No. 501, cotype, skull No. 1445, Amer. Mus. Nasals elongate and square distally, horns short, of oblique oval basal section, overhanging the maxillæ, or projecting forwards or outwards. Incisors, $\frac{1}{3}$. Canines short, tetartocones of premolars moderately developed.

These skulls were previously confused by the writer with *T. trigonoceras*, from which they are readily separated by the horn section, which relates them to some of the primitive types of *M. brachycephalus* and equally to *M. robustus*. The canines are more obtuse than in *M. dispar*, and the superior

incisors resemble those in *Brontotherium* rather than in *M. robustus*.

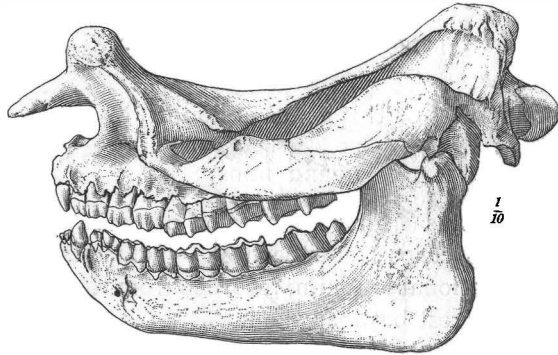


Fig. 6. *Megacerops marshi*. (Amer. Mus. Nat. Hist. No. 501; jaw No. 516.) Type. This skull was figured by Osborn (1896, p. 181) as *Titanotherium trigonoceras*.

Megacerops robustus Marsh.—Type in Yale Museum. Numerous skulls in the American, Princeton, and National Museums. Recorded by Hatcher from very summit of the Upper Beds. In skull development this represents an extreme evolution of the *M. brachycephalus*-*M. dispar* series. It is, however, distinguished from *M. dispar* by the presence of diastemata behind the canines, retarded development of the tetartocones on the superior premolars, broadly transverse horn-section, procumbent position of the horns.

The above-described new species, *M.* (? *Diploclonus*) *bicornutus*, from the Middle Beds is possibly a connecting form between *Megacerops* and the aberrant species from the Upper Beds termed *Diploclonus amplus* by Marsh. The latter is distinguished by short, divergent horns of peculiar triquetrous section, with incisors $\frac{1}{7}$, and elongate canines flattened posteriorly. The animals called *Allops* are certainly more closely related to *Megacerops* than to either *Titanotherium*, *Symborodon*, or *Brontotherium*, but their phyletic position is uncertain.

GENUS ALLOPS MARSH.

Syn. ? *Diploclonus* Marsh.

Canines lanceolate, flattened posteriorly, incisors $\frac{1}{7}$. Horns with greatest diameter progressively transverse, pointed outwards and forwards.

The distinctness of this genus is doubtful.

UPPER BEDS.

Allops serotinus *Marsh.*—Superior premolars with small postero-internal cusps (tetartocones). Represented by two skulls in the National Museum, recorded from the Upper Beds. No connecting crest between the horns.

Allops crassicornis *Marsh.*—Type No. 4289, Nat. Mus. Superior premolars with large postero-internal cusps; cingula

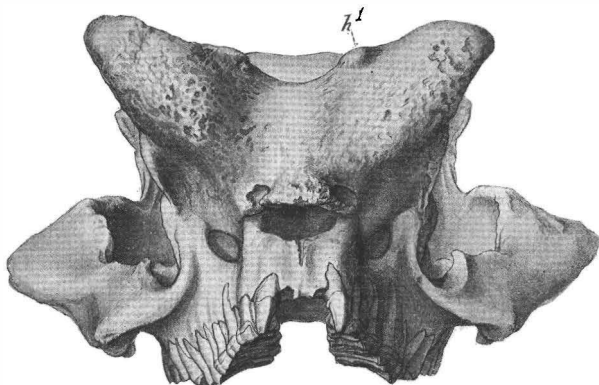


Fig. 7. *Diploclonus amplus* (Marsh). (Yale Museum.) Type. $\times \frac{1}{2}$.

more prominent; zygomata with flattened buccal processes. No connecting crest between the horns.

Allops amplus *Marsh.*—Type in Yale Museum. Characters similar to the above with the exception of a strong connecting crest between the horns and a pair of rugose internal hornlets on the horns, hence the term 'Diploclonus.' It is possible that this species descended from *M.*

bicornutus as a member of a collateral phylum distinguished by internal hornlets. In such case *Diploclonus* may prove to be a valid subgenus.

Phylum III.

Medium-sized Titanotheres with long horns placed more directly above the orbits, of deep anteroposterior diameter at the base, oval at tip; connecting crest feeble or wanting. Nasals thin; skull proportion varying in the species. Incisors degenerate. Canines very small, approximated.

GENUS SYMBORODON COPE.

Syn., *Anisacodon*, *Diconodon* Marsh.

This genus is characterized from the types of *S. torvus*, *S. acer* in the American Museum, and of *S. montanus* in the Yale and National Museums. It is known only from the Middle and Upper Beds, but is entirely distinct. It agrees with *Titanotherium* in the disappearance of incisor teeth, but differs from it absolutely in the horn and nasal structure. It is also widely separate, both in cutting teeth and horn structure, from *Megacerops* and *Brontotherium*.

PROBABLY UPPER BEDS.

Symborodon torvus Cope.—Brachycephalic, incisors ♀, nasals thin, buccal processes of zygomata broad and flat, occipital pillars broad.

Symborodon acer Cope (Syn., *S. altirostris* Cope).—Dolichocephalic, nasals thicker, abbreviated. Horns of male long, recurved, low connecting crest, incisors vestigial.

MIDDLE AND UPPER BEDS.

Symborodon montanus Marsh.—Type in Yale Museum. Nasals thin, of medium length, upper incisors vestigial.

Two skulls in the National Museum (Nos. 4711, 4705) exhibit smaller canines than in Marsh's type, and possibly represent a fourth species,

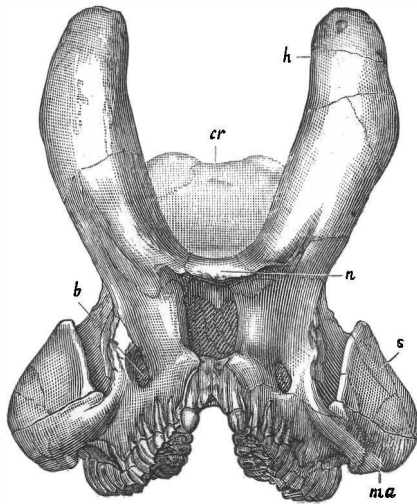


Fig. 8. *Symborodon? montanus* (Marsh). (U. S. Nat. Mus. No. 4711, Sk. V¹.)

because the canines are exceptionally small, the nasals excessively thin, the horns elongate, set wide apart and very far back, oval in section at the top.

Phylum IV.

Titanotheres attaining the largest size, with vertex of cranium greatly elongated by extension of horns in front of orbit and of occiput behind zygomata. Skull, however, as measured along the basal line

and across the zygomata progressively brachycephalic. Horns transverse oval in section from base to summit, shifting forward and progressively elongating and flattening. Nasals abbreviating. Incisors $\frac{2}{2}$. Canines stout, blunt, obtuse. Premolars $\frac{4-3}{4-3}$, cingulum degenerating.

GENUS BRONTOTHERIUM MARSH.

Syn., *Titanops* Marsh.

The type of this genus is the *Brontotherium gigas* jaw (Yale Museum), with which the type jaw of *Titanops elatus* (Yale Museum) is practically identical. The succeeding species (*B. curtum*, *B. ramosum*, *B. dolichoceras*, *B. platyceras*) of very long, flat-horned Titanotheres therefore belong to *Brontotherium*.

A discovery of great interest is a very primitive skull of

the same general type, but with rudimentary horns, in the Lower Beds, to which the name *B. leidy* may be given. A

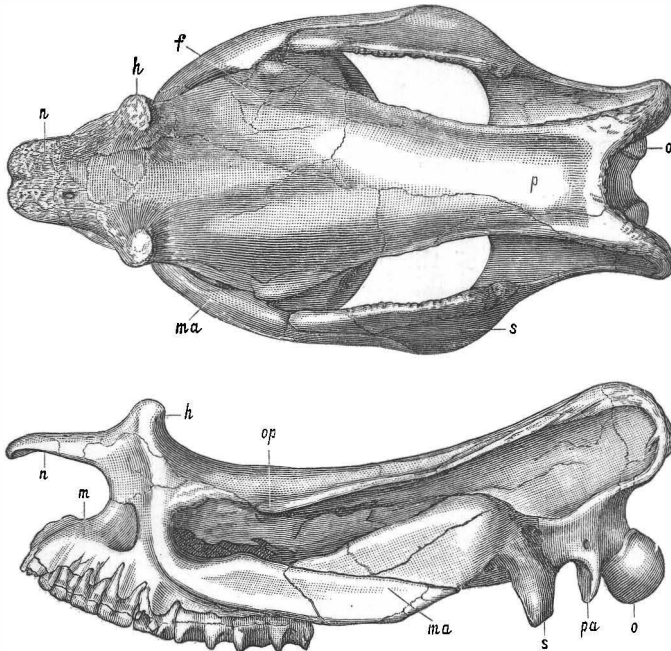


Fig. 9. *Brontotherium leidy*. (U. S. Nat. Mus. No. 4249, Sk. R.) Type. $\times \frac{1}{4}$. The side view of this skull was figured by Marsh (Amer. Jour. Sci., Oct., 1887) as *Menops varians*

successor of this species from the Middle Beds proves to be identical with Cope's *Symborodon hypoceras*.

LOWER BEDS.

***Brontotherium leidy*, sp. nov.**

Type, Skull No. 4249, U. S. Nat. Mus. Nasals elongate, narrowing anteriorly. Horns very short, slightly recurved, of transverse oval section. Canines stout and blunt. Premolars non-cingulate, with rounded contours and well-developed tetartocones. Incisors $\frac{2-1}{1}$.

This rare skull was discovered by Hatcher and is positively recorded from the Lower Beds, Middle Level. It is

of exceptional importance because it is so clearly distinct from its contemporaries in the Lower Beds, namely, *Titanotherium heloceras* and *Megacerops brachycephalus*. It has numerous resemblances in the shape of the nasals, horns, canines, and back of the occiput to the great *Brontotherium* of the Upper Beds.

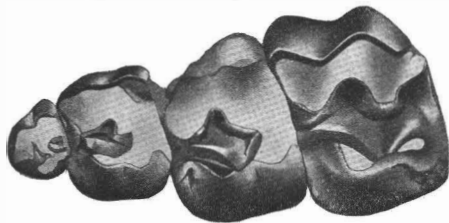


Fig. 10. *Brontotherium leidyi*. (U. S. Nat. Mus. No. 4249, Sk. R.) Type.

MIDDLE BEDS.

B. hypoceras Cope.—Cope's extremely fragmentary type of this species (No. 6361, Amer. Mus., Cope Coll.) is happily supplemented by two skulls found by Hatcher (Nos. 4702, 4273, U. S. Nat. Mus.), one of which is complete though crushed. These prove that this animal is undoubtedly a successor of *B. leidyi*, but separated by certain progressive characters, such as the more anterior position of the horns, and the entire loss of the median incisors.

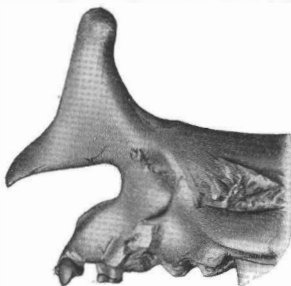


Fig. 11. *Brontotherium hypoceras*. (U. S. Nat. Mus. No. 4273), cotype.

Specific Characters.—Horns of medium length, transverse oval section; nasals shorter than in *B. leidyi*; zygomata with flattened buccal processes; incisors reduced to $\frac{1}{2}$.

This species, although exhibiting generic resemblances, is not ancestral to *B. gigas*.

UPPER BEDS.

The following species, beginning with *B. gigas*, form a closely related progressive series which is chiefly confined to the Upper Beds. One of the most distinctive characters is

the persistence of the large pair of upper incisors in all the male specimens thus far observed. Certain females apparently lack incisors. The horns are very long; the nasals gradually disappear.

B. bucco Cope.—

In the writer's first review the type of this species was confused with the types of *Symborodon torvus*. It is actually represented by the posterior portion of a cranium in the American Museum (No. 6346). The buccal section of the zygomata is more convex than in the succeeding species.

B. gigas Marsh. (Syn., *Titanops elatus* Marsh).—This is now

one of the best-known species, including the type in the Yale Museum, and numerous specimens in the American and National Museums previously referred to *B. elatum*.

Smaller and somewhat more primitive varieties of *B. gigas* are recorded by Hatcher from the Upper Levels of the Middle Beds.

B. dolichoceras Scott & Osborn. (Syn., *Titanops medius* Marsh).—Represented by types in the Harvard and National Museums. This species is intermediate in many characters between *B. gigas* and *B. curtum*.

B. curtum Marsh. (Syn., *Menodus peltoceras* Cope).—The type in the Yale Museum is supplemented by the female horns named by Cope *Menodus peltoceras*, also by

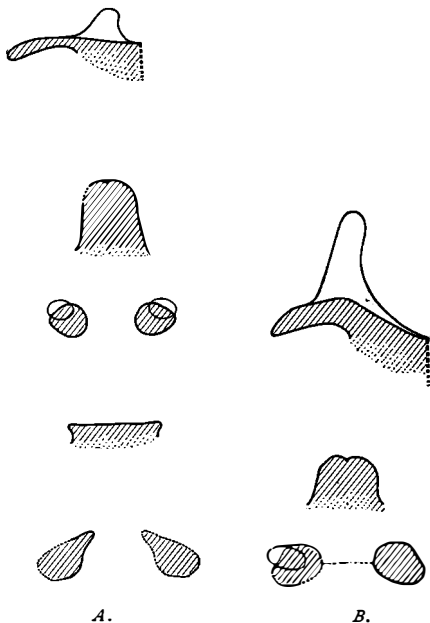


Fig. 12. Sections of nasals, horns, occiput, zygomata. A, *Brontotherium leidy*, type. B, *Brontotherium hypoceras*, cotype.

several specimens in the American, Harvard, and National Museums.

B. ramosum *Osborn*.—There is some question whether this is really distinguishable from *B. curtum*.

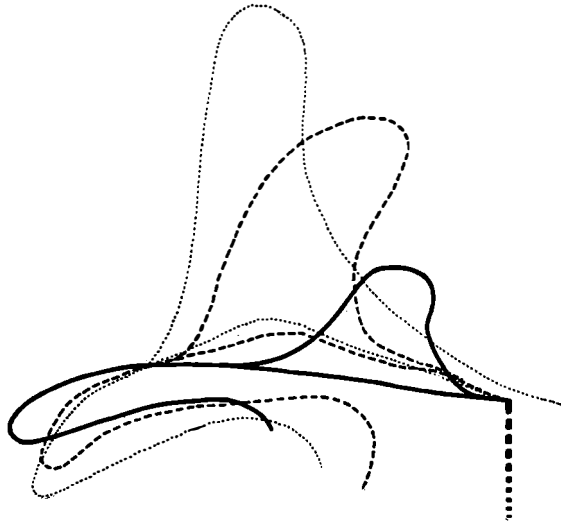


Fig. 13. Comparative fronto-nasal sections and horn contours. Showing progressive shifting forward of horns, and abbreviation of free portion of nasals. *Brontotherium leidy*, Lower Beds. *Brontotherium hypoceras*, Middle Beds. (Nat. Mus. No. 4702.) *Brontotherium hypoceras*. (Nat. Mus. No. 4273.) The dotted vertical line shows the position of the orbit.

B. platyceras *Scott & Osborn*.—Type in the Harvard Museum.

BIBLIOGRAPHY.

- 1887.—SCOTT, W. B., and H. F. OSBORN. Preliminary Account of the Fossil Mammals from the White River Formation contained in the Museum of Comparative Zoölogy. [Titanothera Contributions No. 1.] *Bull. Mus. Comp. Zool.*, Vol. XIII, No. 5, pp. 151-171, pll. I-II, Aug., 1887.
- 1893.—HATCHER, J. B. The Titanotherium Beds. *Amer. Nat.*, March 1, 1893, pp. 204-221.
- 1895.—OSBORN, HENRY F. Perissodactyls of the Lower Miocene White River Beds. [Titanothera Contributions No. 2.] *Bull. Amer. Mus. Nat. Hist.*, Vol. VII, Art. XII, pp. 343-375, pll. VIII, IX, Dec. 23, 1895.

-
- 1896.—OSBORN, HENRY F. The Cranial Evolution of Titanotherium. [Titanothere Contributions, No. 3.] *Bull. Amer. Mus. Nat. Hist.*, Vol. VIII, Art. IX, pp. 157-197, July 31, 1896.
- 1900.—OSBORN, HENRY F. Phylogeny of the Rhinoceroses of Europe. *Bull. Amer. Mus. Nat. Hist.*, Vol. XIII, Art. XIX, pp. 229-267, Dec. 11, 1900.
- 1902.—OSBORN, HENRY F. Dolichocephaly and Brachycephaly in the Lower Mammals. *Bull. Amer. Mus. Nat. Hist.*, Vol. XVI, Art. VII, pp. 77-89.