Article IX.—THE CRANIAL EVOLUTION OF TITANOTHERIUM.

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WITH PLATES III AND IV, AND FIFTEEN FIGURES IN THE TEXT.

The rapid evolution of the Titanotheres during the deposition of about 180 feet of sediment in the Oligocene White River Beds is one of the striking chapters in mammalian history which is still only partly understood.

The following study of the evolution of the cranium is chiefly an attempt to distinguish the influences of *sex*, of *age* or *growth*, and of *individual variation* from the truly *retrogressive* and *progressive* characters. It is written to this end, but unfortunately we cannot intelligibly treat the morphology of *Titanotherium* without first clearing out the Augean stable of nomenclature. The greater number of the *thirteen* generic and *thirty-one* specific terms which have been proposed are either undefined or undefinable, or are based upon non-specific or non-generic characters.

The materials examined in connection with this study are: Cope's type skulls and jaws now in the American Museum collection; eighteen skulls mostly collected, partly purchased, for the Museum in the expeditions of 1892 and 1894 by Dr. Wortman and Mr. Peterson; the three type skulls in the Harvard University Museum; the few skulls belonging to the U. S. Geological Survey collection[1] in the National Museum at Washington. The author is indebted to Dr. W. D. Matthew for notes upon Marsh's type skulls in the Yale University Museum, also for much valuable assistance.

The illustrations are the work of Rudolph Weber. The majority of the type skulls are shown in the two plates.

[1] These skulls are partly determined by Prof. Marsh. By his direction the cases containing them are kept closed, so that only part of their characters can be observed.

I.—Systematic Introduction.

Historical Notes.

In 1847 (1) Dr. Hiram A. Prout, of St. Louis, described and figured part of a lower jaw containing the true molars of a huge animal which he supposed to be *Palæotherium*. This specimen, as Leidy later remarked in his 'Ancient Fauna of Nebraska' (p. 72), is noteworthy as "the first fossil from the Eocene cemetery of Nebraska, presented to the notice of the world." In 1849 Pomel (2) recognized the distinct generic character of this jaw and termed it *Menodus*, a term which is technically preoccupied and therefore not employable.[1] In 1850 the same jaw was termed *Palæotherium proutii* by Owen, Norwood and Evans (3), without definition. Shortly afterwards Leidy (4) gave the name *P. bairdii* to another specimen. In 1850 Leidy (5) mentioned one other specimen as *P. giganteum*. In 1852 (7) he partially defined the species *T.* (*Rhinocerus*) *americanus* (Pl. XVII, Figs. 1–4). In the same memoir of 1852 Leidy also first used the name *Titanotherium* without definition, but in 1853 he (8) fully described and figured the jaw in the Owen Collection (Anc. Faun. Neb., Pl. XVI, p. 551, Fig. 1) as the type of the new genus *Titanotherium*, mentioning a third species *T. maximum*.

This established the genus. *None of the above species are determinable.* The terms *T. proutii* and *T. americanum* have been variously cited by Marsh, Cope, Scott and Osborn, but are of no specific value whatever; the lower teeth and jaws upon which they are based are incomplete and uncharacteristic; the types have been partly destroyed by fire.[2]

The upper teeth and skull were still unknown. In 1859 Leidy (9) described the palate and superior molars (found by Meek and Hayden in Nebraska, now in the Hall Collection, American Museum of Natural History) as those of a huge *Anoplotherium*.

[1] As Marsh noted in 1873, "The generic name *Titanotherium* Leidy is antedated by *Menodus* Pomel (Bib. Univ. de Geneve, X, p. 75, Jan., 1849). The latter, however, is essentially the same word as *Menodon*, von Meyer, 1838. Hence *Titanotherium* should be retained."

[2] Prout's collection was partly burnt in Burlington, Iowa. A portion of it went to Chicago and was destroyed in the Chicago fire.

TABLE I.—CHRONOLOGICAL LIST OF TERMS.

(1)	Palæotherium	*Prout*	Am. Jour. Sci., 1846, II, p. 288; 1847, p. 248.
(2)	Menodus	*Pomel*	Bib. Univ. de Geneve, X, p. 75, Jan., 1849.
(3)	Palæotherium proutii	*Owen*	Owen, Norwood, Evans., Proc. Acad. Nat. Sci., 1850, p. 66.
(4)	" bairdii	*Leidy*	" " " " " " " p. 122.
(5)	" giganteum	"	Owen's Rep. Geol. Surv. Wisc., Ref. to Pl. XIIB, figs. 3, 4.
(6)	Titanotherium (Rhinocerus) americanus	"	Proc. Acad. Nat. Sci., 1852, p. 2.
(7)	" proutii	"	Anc. Faun. Neb., 1853, p. 76 (Owen's Rep., p. 551).
(8)	" maximum	"	" " " p. 78.
(9)	Anoplotherium	"	Ext. Faun. Dak. and Neb., 1859, p. 206.
(10)	Leidyotherium	*Prout*	Trans. Acad. St. Louis, 1860, p. 699.
(11)	Megacerops coloradensis	*Leidy*	Proc. Acad. Nat. Sci., 1870, p. 1.
(12)	Brontotherium gigas	*Marsh*	Am. Jour. Sci., June, 1873, p. 486.
(13)	Symborodon torvus	*Cope*	Palæon. Bull. No. 15, Aug. 20th, 1873, p. 2.
(14)	" (Miobasileus) ophryas	"	" " " " p. 3.
(15)	Megaceratops acer	"	" " " " p. 4.
(16)	" heloceras	"	" " " " p. 4.
(17)	Symborodon bucco	"	Syn. New Vert. Tert. Col., Oct., 1873, p. 10.
(18)	" altirostris	"	" " " " p. 12.
(19)	" trigonoceras	"	" " " " p. 13.
(20)	Brontotherium ingens	*Marsh*	Am. Jour. Sci., Jan., 1874, p. 85.
(21)	Symborodon hypoceras	*Cope*	Bull. U. S. Geol. Surv. Terr., 1874, p. 491.
(22)	Anisacodon montanus	*Marsh*	Am. Jour. Sci., 1875, p. 246.
(23)	Diconodon *non* Anisacodon	"	" " 1876, p. 339.
(24)	Menodus angustigenis	*Cope*	Ann. Rep. Geol. Surv. Can., Jan., 1896, C., p. 81.
(25)	" tichoceras	*Scott & Osborn*	Bull. Mus. Comp. Zoöl., 1887, August, p. 159.
(26)	" dolichoceras	"	" " " " p. 160.
(27)	" platyceras	"	" " " " " "
(28)	Brontops robustus	*Marsh*	Am. Jour. Sci., Oct., 1887, p. 326 (Sept. 24th).
(29)	" dispar	"	" " " p. 327.
(30)	Menops varians	"	" " " p. 328.
(31)	Titanops curtus	"	" " " p. 330.
(32)	" elatus	"	" " " p. 330.
(33)	Allops serotinus	"	" " " p. 331.
(34)	Haplacodon angustigenis	*Cope*	Am. Nat., 1889, March, p. 153. (*bis*).
(35)	Menodus selwynianus	"	" " July, 1889, p. 628.
(36)	" syceras	"	" " " " "
(37)	Diploclonus amplus	*Marsh*	Am. Jour. Sci., June 1890, p. 523.
(38)	Teleodus avus	"	" " " p. 524.

In 1860 Prout (10) proposed to make the same specimen the type of a new genus *Leidyotherium*. Leidy soon rectified his mistake, referring this palate to *T. proutii*, but even in his great memoir of 1869 he placed *Titanotherium* in the Anthracotheriidæ. In 1870, still ignorant of the upper skull structure, Leidy (11) described the horns and nasals sent to him from Colorado as *Megacerops coloradensis*, a form which he, in common with Cope and Marsh, believed to be related to the Dinocerata.

Between 1870 and 1873 the explorations of Marsh and Cope in Colorado yielded a series of skulls and limbs, and established these animals definitely as a distinct family of Perissodactyla (see Marsh, Am. Jour. Sci., June, 1873). Marsh (12) founded his first species upon a jaw and dentition, also from Colorado, to which he gave the name *Brontotherium gigas*. He distinguished the genus from Leidy's *Titanotherium* by the presence of but *three* lower premolars. We have seen, however, that Leidy's generic type only contained the four back teeth, P4 to M3, and we now know that the number of lower premolars is subject to individual variation, for some animals have three premolars upon one side and four upon the other side of the jaw. The generic distinction is therefore invalid, while the species *T. gigas*, although founded upon a fine jaw, awaits correlation with a skull before it can be defined. We are indebted to Marsh for the first complete outline of the main characters of the family, in his article of 1873 'On the Structure and Affinities of the Brontotheriidæ."[1] Shortly after *Brontotherium* was proposed, Cope (13) (Aug., 1873) proposed[2] a fourth genus, *Symborodon*, selecting as types "mandibular rami only, which cannot be certainly associated with crania," and distinguishing the genus by the supposed absence of lower incisors and by the presence of but three lower premolars. With his type species *S. torvus* (13) were found three other species, in which he did not at first recognize the Titanothere kinship, namely : *Miobasileus ophryas* (14), *Megaceratops acer* (15), *Megaceratops heloceras* (16). The first named, *M. ophryas*, was established upon a cranium, and proposed as the type of a fifth genus, *Miobasileus*, since abandoned by Cope. In October, 1873,[3]

[1] Am. Jour. Sci. and Arts, 1873, p. 486.
[2] Pal. Bull. No. 15, Proc. Am. Phil. Soc., August 20, 1873, p. 2.
[3] Synopsis of New Vertebrata from the Tertiary of Colorado (*S. ophryas*), Oct., 1873.

Cope referred to *Symborodon* all the preceding as well as the additional species ; (17) *S. bucco*, as the largest type of the genus; (18) *S. altirostris*, distinguished by the elevated position of the snout and horns ; *S. trigonoceras* (19), distinguished by the short, stout, triquetrous horns.

In January,[1] 1874, Marsh (20) gave the full account of the family above referred to, and proposed the species *Brontotherium ingens* upon a nearly complete skull and jaws. In July, 1874, Cope's 'Report upon the Vertebrate Palæontology of Colorado"[2] contained a full description of the chief characteristics of the family and an analysis of all the species of *Symborodon*, together with the definition of the new species *S. hypoceras*.[3]

All the above specimens, excepting Leidy's original generic type jaws, were found in the Oligocene of Colorado. In 1875[4] Marsh described his collections of 1874 in Dakota and Nebraska and proposed the sixth new genus *Anisacodon* (22), distinguished by three lower premolars and the last upper molar with two cones, the type species *A. montanus* (22) being a skull from Nebraska. In April, 1876, this was re-named *Diconodon*; (23) the principal characters of the family were again discussed, and the types of *B. gigas*, *B. ingens* were figured.[5] In 1886 Cope described the *M. angustigenis* (24) from Canada. Thus the matter rested until August, 1887, when Scott and Osborn[6] reviewed the family and described the collection made for the Harvard University Museum by Garman in Dakota. They revived the term *Menodus* and proposed the new species: *M. tichoceras* (25), *M. dolichoceras* (26), and *M. platyceras* (27), accompanied by a restoration of *M. proutii*. In the meantime Hatcher had brought together for the U. S. Geological Survey a remarkable series from Dakota and Nebraska, which together with skulls from Colorado formed the basis of a further contribution from Marsh.[7] He proposed first the genus *Brontops*, from the type species, *B. robustus*, from northern Nebraska, and the smaller species *B. dispar* from Dakota ; second, the genus *Menops*, from the type, *M. varians*, and the genus *Tita-*

[1] Am. Jour. Sci., Jan., 1874, p. 6.
[2] Bull. U. S. Geol. Surv. Terr., 1873 (publ. 1874), pp. 427–533.
[3] Op. cit., p. 491.
[4] Am. Jour. Sci., March, 1875, p. 245.
[5] Am. Jour. Sci., 1876, p. 335.
[6] Bull. Mus. Comp. Zoöl., Vol. XIII, 1887, p. 157.
[7] Am. Jour. Sci., Oct., 1887, pp. 326–331.

nops from the type skull of *T. curtus* found in Colorado, and a second species *T. elatus*, from Dakota; fourth, the genus *Allops*, from the type skull *A. serotinus* found in Dakota.

In 1889 Cope proposed the genus *Haplacodon* (34) from his Canadian Survey species, *M. angustigenis*,[1] and added the two additional species *M. selwynianus* (35) and *M. syceras* (36). His latest additions are found in his report[2] from the Oligocene of the Cypress Hills, Canada, in which he further characterizes the three new species above referred to.

The latest genus to be added to the long series is *Teleodus* (37), characterized by Marsh[3] as having *three* lower incisors, and believed by Hatcher to come from the lowest beds, also to possess a trapezium.

It is obvious that the only method of clearing up this heterogeneous list is first to establish certain laws of cranial development, and second, to apply these laws to the distinction of the genera and species in chronological order. Examined in this way, the vast array of genera and species are resolved into one or possibly two genera, and about fourteen definable species.

II.—Principles of Cranial and Dental Evolution.

The main characters hitherto used in definition by Marsh and Cope, Scott and Osborn, are :

A. Number of incisors and of premolars. (Cope, Marsh.)

B. Development of a cingulum upon the premolars. (Cope, Marsh.)

C. Presence of a second cone upon last superior molar. (Marsh.)

D. Length and shape of nasals. (Cope, Marsh, Scott, Osborn.)

E. Length and shape of horns. (Cope, Marsh, Scott, Osborn.)

F. Presence or absence of a trapezium. (Hatcher.)

[1] Am. Nat., 1889, p. 628.
[2] Contr. to Canadian Palæontology, Vol. III, p. 9.
[3] Am. Jour. Sci., June, 1890, p. 524.

The principles of cranial evolution which put these characters to the test and determine which are valid and which invalid, may be considered under ten heads: 1. General increase of size. 2. Dental series as a whole. 3. Horns. 4. Nasals. 5. Zygomatic arches. 6. Auditory meatus. 7. Cingula. 8. Incisors. 9. Canines. 10. Hypocone.

1. *General Development in Ascending Geological Levels.*

PROGRESSIVE.	RETROGRESSIVE.
1. General increase in size of skull and skeleton.	2. Dental series relatively arrested or retrogressive in development.
3. Horns elongating in males. *a*. Shifting forwards to absorb nasals. *b*. Long axis altering from antero-posterior to transverse plane. *c*. Acquiring a transverse connecting crest, uniting them at the base.	4. Nasals degenerating in both sexes to reduced knobs. No sexual differences apparent.
	9. Trapezium disappearing at an early period.
5. Zygomatic arches spreading.	8. Incisors becoming variable at an early period, especially in females.
6. Post-glenoid and post-tympanic processes uniting.	7. Premolar cingula reduced in latest stages.
6*a*. Occiput broadening and becoming more robust; superior border becoming deeply concave.	7*a*. First lower premolar becoming variable.

12. Third trochanter developing.[1]

2. *Growth and Age Characters common to both Sexes and all Geological Levels.*

1. Increasing rugosity of the skull, arches, horns and nasals.

8. Loss of variable and vestigial teeth, incisors and premolars in old age.

11. Anterior caudal[2] uniting with sacrum to form four sacrals.

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[1] Teste Hatcher, Am. Nat., March, 1893, p. 216.

[2] Teste Hatcher, Am. Nat., March, 1893, p. 217.

TABLE II.—MEASUREMENTS OF SKULLS AND TEETH.

	Catalogue Number of Specimen.	Length of Skull.		Width across Zygomatic arches.	Length of Molar-Premolar Series.		Occiput.[1]		Horns.[2]		Nasals.[3]
		Condyle to tip of Premax.	Occiput to tip of Nasals.		p^1–m^3.	p^{1-4}	Height.	Breadth	Length.	Spread.	Free Length.
T. heloceras	6360	.637	.652	.393	.287	...	.175	.169	.126	.280	
T. trigonoceras, Type	6355	....	.765	.485	....	....	.172	.266	.145	.348	.141
T. trigonoceras	6356	...	...	..	.354	.130	...	....	.150	.358	.130
T. trigonoceras	501	.675	.705	.452	.314	.125	.225	.278	.130	.280	.100
T. trigonoceras	1445	.680	.680	.470	.345	.135	.222	.276	.111	.280	.100
T. ingens, Type	....	....	.915[4]	.558	.428	.162	....	....	....	.507	
T. ingens ♂	505	.805	.780	.546	.398	.150	.247	.325	.192	.494	.126
T. ingens ♂	1066	.770	.830	.550	.365	.135	.225	.335	.183	.435	.122
T. ingens ♀	1067	.730	.820	.440	.355	.140	.265	.260	.214	.480	.127
T. ingens ♀	506	.805	.770	....	.410	.151	....	....	.175	...	.135
T. (bucco) torvum	6345	.665	.813	.660	.291	....	.225	.330	?.210	?.361	.090
T. (bucco) torvum	6346	....	....	.670	....	....	.300	.325			
T. robustum ♂	1083	.758	....	.600	.365	.141	....	....	.150	.355	.090
T. robustum ? ♂	1069	.833	.830	.645	.380	.145	.390	.170	.130	.324	.096
T. robustum	1082	.767	.835	.652	.355	.132	.235	.355	.178	.378	?.085
T. robustum ♀	518	.825	.835	.557	.408	.165	.240	.356	.110	.300	.075
T. torvum (robustum)	1081	.707	.767	.610	.367	.139	.250	.320	.231	.307	.066
T. dolichoceras	520	.720	.850	.565	.330	.132	.215	.345	.145[1]	.422[1]	.068
T. elatum ♂	492	.880	.930	.737	.362	.125	.285	.440	.361	.566	.100
T. elatum ♂	1070	....	....	....	...	.132	....	....	.240	.418	.090
T. elatum ♀	1005	.690	.673	.540	.346	.135	.203	.292	.142	.287	.047
T. elatum ♀	1006	.720	.740	.490	.335	.126	.265	.300	.155	.290	.073
T. amplum (elatum) ♀	1008	.735	.781	.495	{.365 / .340}	....	....	....	.233	.340	.040
T. acer ♂, Type	6348	....	.680	....	....	....	.235	....	.290	.350	.061
T. (altirostris) acer ♀	6350	.634	.645	....	?.330	...	.245	....	?.141		
T. acer ♀	6349	.635	.655	....	.335	.130	.235	.185	.178	.290	.050
T. ramosum ♂, Type	1447	.742	.820	.774	.360	.131	.250	.400	.399	.635	.049
T. platyceras ♂	1448	.730	.858	.815	.342	.123	.280	.455	.433	.620	.019

[1] In several cases these measurements are approximate, owing to crushing.
[2] This measurement is taken down the outer side of the horn to the anterior nares.
[3] This is the free portion of the nasals as seen in profile.
[4] Lineal measurement taken from condyle to tips of nasals.

3. *Sexual Characters, common in all Species, especially in the Higher Geological Levels.*

	MALE.		FEMALE.
1.	Skulls of greater dimensions.	1.	Skulls of smaller size.
3.	Horns, especially in upper beds, very long and powerful.	3.	Horns shorter, often imperfectly ossified at the tips.
3*a*.	Transverse connecting crest very prominent in higher levels.	3*a*.	Transverse crest somewhat less prominent.
5.	Zygomatic arches widely extended into buccal plates.	5.	Zygomatic arches less widely expanded.
1.	Occiput with stout lateral pillars and broad rugose upper border (in upper beds).	1.	Occiput less robust.
9.	Canines robust.	9.	Canines smaller, pointed.
8.	Incisors larger and more constant.	8.	Incisors more variable, smaller.

Hatcher[1] has placed 'delicate nasals' and a 'feebler internal cingulum' upon the premolars among the female characteristics. Our observations do not confirm this; these structures are apparently independent of sex.

4. *Individual variations observed in members of the same sex and species.*

8. Incisors sometimes constant, sometimes entirely wanting or unequal in number upon opposite sides of the skull, varying from 2 to 1 to 0.
7. Premolar 1 variable, sometimes present upon one side and wanting upon the other side of the jaw.
10. Second internal cone upon last superior molar inconstant in members of the same species.
7. Internal cingulum upon premolars variable.

A comparison of the figures upon Plates III and IV shows the rapid increase in size. The Titanothere skull development in general is marked (*a*) by the forward movement of the orbit; (*b*) the great backward elongation of the skull and temporal fossæ; (*c*) in the occiput the deep excavation of the superior border, the development of lateral pillars, and of the superior rugose crest; (*d*) closure of the external auditory meatus inferiorly.

[1] Am. Nat., March, 1893, p. 216.

5. *Influences of Age, Sex, Growth and Variability.*

1°. GENERAL LAWS OF GROWTH.—In the accompanying Table II the species are arranged approximately in the order of evolution, taking *T. heloceras* as the least specialized and *T. platyceras* as the most specialized types.

The skull gains only 10 or 20 centimeters in *length*, while it doubles in *width*, gaining 400 centimeters.

The premolar-molar series rapidly increases in length, and then as rapidly diminishes, so that the grinding area is no larger in the very large animals (*T. platyceras*) of the upper beds than in the small animals (*T. trigonoceras*) of the lower beds.

The occiput gains about 10 centimeters in height and nearly 30 in breadth.

The horns increase to three or four times their original length while the nasals diminish to one-sixth their original length.

2°. ARRESTED GROWTH OF THE TEETH.—1 & 2. The general increase in the size of the skull and body is not accompanied by a corresponding increase in the dental series. Table II shows that the premolar-molar series reach their maximum in the characteristic species of the middle beds, namely, *T. ingens*, and then actually decline, so that in the enormous animals of the highest beds the dental series has relatively less volume than in the comparatively small creatures of the lower beds. This arrested tooth development may have been a factor in extinction. An exactly analogous fact is observed in the Dinocerata.

3°. HORNS. The whole skull structure is mainly secondary to the horns. The successive stages in the form and position of the horns are therefore highly characteristic.

1st Stage.—In *Telmatotherium*[1] and *Diplacodon*[2] they arise at the junction of the fronto-nasal suture, slightly in front of the orbits, overhanging the sides of the face. The primitive horn section is therefore an *antero-posterior oval*, and the longest diameter of all of the earliest horn types is parallel with the long axis

[1] Osborn, 'Fossil Mammals of the Uinta Basin.' Bull. Am. Mus. Nat. Hist., 1895. p. 91.
[2] Hatcher 'On a New Species of Diplacodon,' Am. Nat., 1895, Pl. XXXVII.

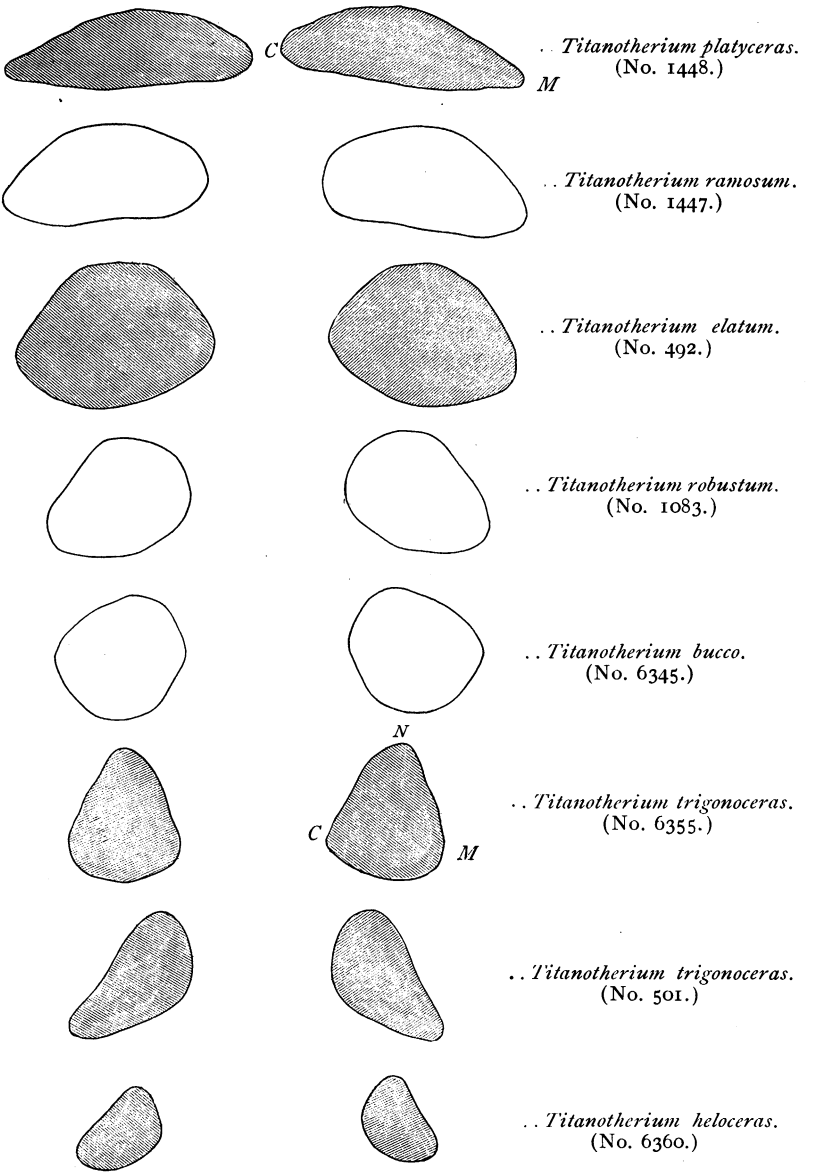


DIAGRAM I.—Horn sections taken just above the base, showing the development from an antero-posterior to a transverse axis. *N*, line connecting with nasals. *M*, line descending to malars. *C*, line entering connecting crest. The anterior face of the horns is above.

of the skull; the anterior edge of the oval extends into the sides of the nasals *N*, the posterior edge dips back to the malars *M*. At the close of this stage the horns acquire a *circular section.*

2d Stage.—A low 'connecting crest' arises between the bases of the horns and gives them a *trilateral section* consisting of an antero-median face, a postero-median face, and an antero-inferior face. Thus all middle horn types are triangular, with an internal angle *C*.

3d Stage.—The horns gradually shift forwards until they directly overhang the anterior nares, and finally the symphysis. They thus *absorb* the nasals and lose their base of support upon the greatly abbreviated maxillaries. Thus disappears the nasal angle *N*; also the antero-inferior or maxillary face, and the horns acquire a *transverse oval* section.

4th Stage.—While the horns flatten, the web, or '*connecting crest*,' between their bases, increases until the horns consist of two recurved plates connected by a broad median crest. This is the final stage, consisting of a "*disc section.*"

There is thus a total change in form and position.

The ontogeny of the horns recapitulates the phylogeny more or less closely in the lower beds only.

Both Marsh and Hatcher have remarked that females are distinguished by smaller horns. But Marsh has not applied this principle in his definitions. The sexual distinctions are as follows:

Female Horns.—In *female* Titanotheres the horns exhibit an *arrested stage of male development.* This is most clearly demonstrated in the comparison of three female skulls (Nos. 1005, 1006, 1008) in the American Museum Collection, with two male skulls (Nos. 492, 1070) of the species *T. elatum.* (See Figs. 9, 10, 11.) In the females the horns are often imperfectly ossified at the tips, sometimes pointed. As the horns evolve in the higher levels the differences between the sexes become more marked, for we observe less wide contrasts in skulls found in the lower beds. As seen in *T. acer*, *T. trigonoceras* and *T. ingens*, the 'connecting crest' is more constant and more pronounced in males than in females.

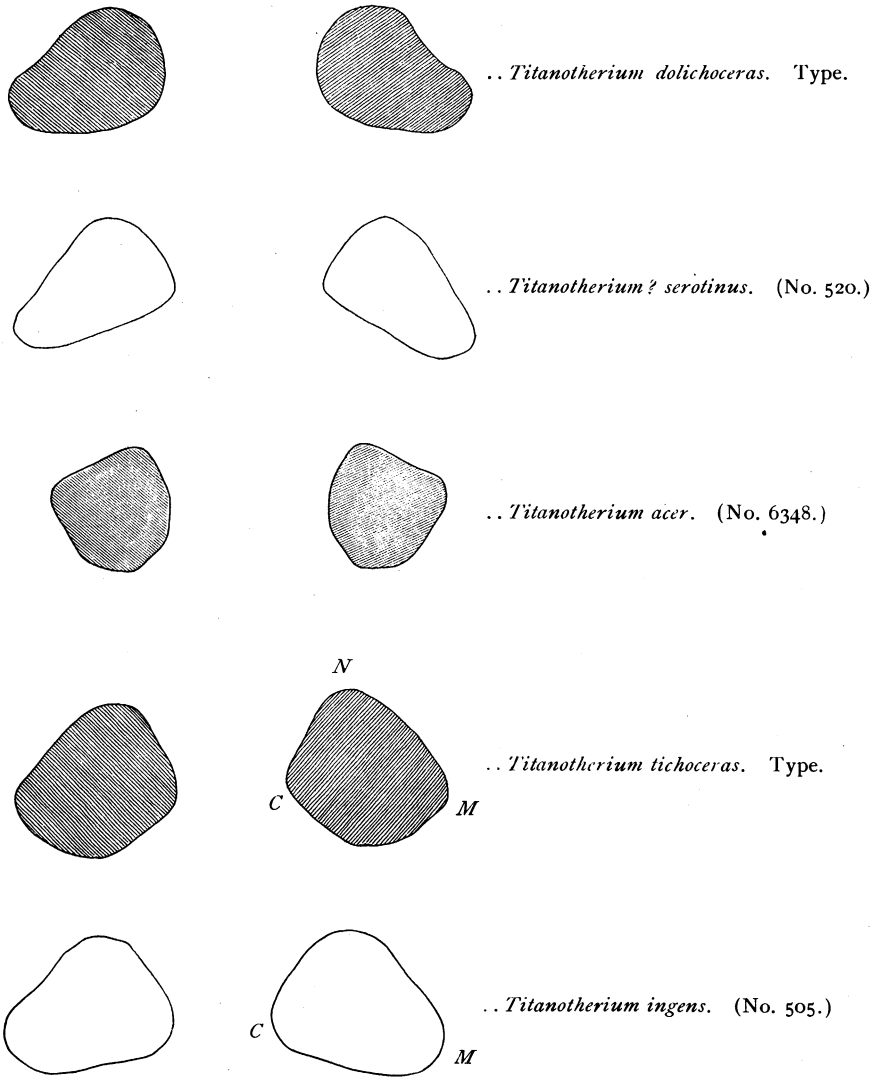


DIAGRAM II.—Horn section taken in the same manner as Diagram I.

Again, among the skulls referred to *T. ingens* (505, 1066, 1067), three have very stout triangular horns, a fourth (506), although a very large animal, has more slender horns, rounder in section, with very slender canines. This is believed to be a female. Similar differences are observed in specimens of *T. trigonoceras*.

Individual Variations.—The appearance of the horns is greatly affected by the stages of growth and by the crushing. There are two cases of *branching* in this collection, a feature considered by Marsh a generic character in his type of *T.* (*Diploclonus*) *amplus*. One case is in the horns of a female of *T. elatum* (1008), another is in an undetermined skull (1081). This character is apparently an individual variation.

4°. NASALS.—The hypertrophy of horns and compensating atrophy of nasals was pointed out by the writer in 1887. It now appears more accurate to state that the horns practically shift forward to the tips of the nasals.

The length and form of the nasals is a characteristic feature of progressive development, and is very slightly if at all subject to sexual variation as believed by Hatcher[1]. In the primitive condition[2] (*Diplacodon*) the nasals are long, and distally broad and truncate. In *T. coloradense* Leidy they taper and are recurved distally. In the *T. trigonoceras* and *T. ingens* skulls they are broad, rugose and often cleft distally. In progressive development they are rapidly reduced in length and tapered so that they finally become short-pointed knobs.

5°. ZYGOMATIC ARCHES.—There is considerable but not absolutely conclusive evidence that the very robust widely spreading zygomatic arches of the latest species are *male* characteristics. In the *T. elatum* series all the skulls with feeble or imperfect horns and small canines have moderately expanded arches, while the old male (No. 492) has enormous cheek bones. In the *T. ingens* series the same difference is observed in a less marked degree. If this character is actually sexual, it is one in which (as in the horns) the males progressively diverged from the females in the evolution of the skull.

[1] Am. Nat., March, 1893, p. 216.
[2] Hatcher, *op. cit.*, Pl. XXXVII.

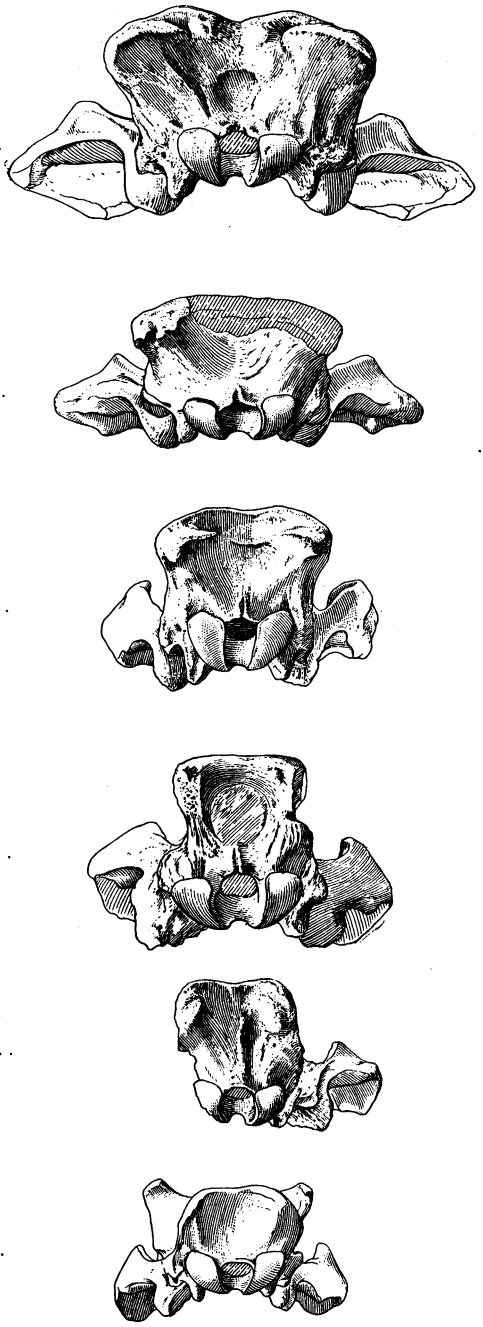


Fig. 1. Exhibiting the evolution of the occiput, the lateral pillars, and incurving of the superior border. One-twelfth natural size.

6°. AUDITORY MEATUS.—The union of the post-glenoid and post-tympanic processes parallels that which we observe in the Rhinoceroses. In the *T. heloceras* skull the external auditory meatus is widely open below. In the *T. platyceras* skull it is reduced to a small foramen enclosed by a solid wall of bone below.

7°. CINGULUM.—The cingula are, upon the whole, retrogressive. They reach their greatest development in *T. ingens*, and then decline.

Our materials do not support Hatcher's[1] supposition that strong cingula are characteristic of male skulls, but prove that the development of the *cingulum is irrespective of sex, partly a matter of individual variation, chiefly of robust dentition.*

It follows that Cope[2] is in error in relying upon the cingulum to divide the Titanotheres into two parallel groups.

Variability.—In two closely similar skulls (Nos. 501, 1445) the internal premolar cingulum is strongly developed, while the external cingulum is feeble in the one (1445) and strong in the other (501).

Independent of Sex.—In the female skull of *T. ingens* (No. 506), the cingula are quite as strongly marked as in the male skulls (Nos. 505, 1066, 1067). In the female skulls of *T. elatum* (Nos. 1005, 1006) the cingulum is as strong or stronger than in the male skulls (Nos. 492, 1070).

Associated with robust dentition.—The only forms in which sharply-defined internal and external cingula upon both upper and lower premolars seem to be characteristic, are the type skull and the American Museum skulls of *T. trigonoceras* and *T. ingens.* As shown by the measurements, this species is characterized by a very robust dentition.

Retrogression.—A comparison of all the earlier with the later types shows that the cingulum reaches its maximum with the species or the middle beds, and then declines. It is variable in *T. robustum* and almost obsolete in *T. acer* and *T. platyceras.*

[1] Am. Nat., March, 1893, p. 216.
[2] Contr. to Canadian Palæontology, Vol. III, 1891, p. 9.

8°. INCISORS.—Individual variability here is very marked, but there seem to be certain underlying principles, such as the following:

Persistence.—So far as the American Museum material is concerned, there is no evidence that the incisors are positively retrogressive, as commonly stated by Hatcher and others, since three heavily horned male skulls of *T. platyceras* and of *T. elatum*, from the topmost strata, present two pairs of full-sized incisors. Marsh[1] also implies that his long-horned specimens (*Titanops*) have two upper incisors.

On the other hand, one of the most primitive skulls (No. 501) of *T. coloradense* presents but one incisor upon each side, and all the skulls in the middle beds (*T. ingens*) of our collection exhibit no incisors at all.

Sex.—Of the supposed females of *T. elatum*, one (1005) has no upper incisors, one (1006) has reduced vestiges of the lateral pair, two (1008, 520) have the outer pair well developed. Marsh's type is said to have two upper incisors. It would appear from this that in this species at least the incisors are more variable and reduced in females than in males.

This evidence is offset by the fact that in all the five, *T. trigonoceras*, *T. ingens* skulls the incisors are vestigial or wanting without distinction of sex. Marsh figures two incisors in dotted outlines, but his type of *T. ingens* entirely lacks the premaxillaries, and therefore gives no evidence. It would appear, however, that in *T. trigonoceras* the incisors are vestigial or wanting in both sexes and in both jaws.

9°. CANINES.—We here derive characters both of sexual and of specific value.

Sex.—The shape of the canines is the same in both sexes, but the male tusks are much more powerful than the female. This is especially marked in the male *T. ingens* (No. 505), in which the tusks are 62 mm. long by 34 mm. diameter at the cingulum, while in the female (No. 506) the canines measure only 40 x 21 mm.

It is also well shown in *T. elatum* in which the female tusks are also two-thirds the size of the male tusks, as observed in a com-

[1] Am. Jour. Sci., Oct., 1887.

parison of five skulls. In the latest types of males the canines are powerful but obtuse.

10°. SECOND INTERNAL CONE OF LAST UPPER MOLAR.—Individual variability here reaches its maximum. This cone, which is well known to occur in the *Palæosyopinæ* of the Bridger, is apparently neither a specific nor progressive character in *Titanotherium*. It is found in all stages of independence from the cingulum in the oldest as well as in the most recent types. It certainly varies within the limits of a single species and sex.

6. *General Conclusions.*

The net result of this examination is that the characters upon which the genera *Symborodon*, *Diconodon*, *Brontops*, *Titanops*, *Allops*, *Haplacodon* and *Diploclonus* are founded, are either marks of sex, age or individual variability, and that these names have no standing whatever. *Teleodus* may prove to be a distinct form, but has not yet been separated generically from *Diplacodon*.

II.—REVISION AND DEFINITION OF SPECIES.

FOR DATES, SEE TABLE I.

Menodus *Pomel.*

Preoccupied by *Menodon*, von Meyer.

3. Titanotherium proutii *Leidy.*

Indeterminate species.

4. Titanotherium bairdii *Leidy.*

Indeterminate species.

5. Titanotherium giganteum *Leidy.*

Indeterminate species.

6. Titanotherium americanum *Leidy.*

Indeterminate species.

8. Titanotherium maximum *Leidy.*

Indeterminate species.

11. Titanotherium coloradense *Leidy.*

PLATE III.

Megacerops coloradensis LEIDY. (Type of genus *Megacerops.*)

Type Loc —Colorado. Level unknown.

Type.—Fractured horns and nasals. Coll. Acad. Nat. Sciences, Phila.

Spec. Char. (of Type).—*Horns* of medium length; section antero-posterior oval or slightly trihedral at base, rounded at summit; directed upwards and outwards; no transverse crest. *Nasals* long, tapering somewhat, decurved and notched at extremity.

The full characters of this species are not certainly known. In the Harvard University Museum is a complete skull in which the corresponding parts are closely but not exactly similar in form and measurement to Leidy's type. This skull,[1] apparently female, exhibits the following characters:

Cranium long and narrow; occiput elevated and slender, narrow, with superior border not incurved; zygomatic arches expanding slightly; external cingulum feeble upon P^{1-3}, strong upon P^{4}, post-glenoid and post-tympanic processes not quite in contact; one superior incisor.

A closely related, if not identical form, is the Canadian Survey specimen, referred to *T. americanum* by Cope.[2]

12. Titanotherium gigas (*Marsh*).

Brontotherium gigas MARSH. (Type of genus *Brontotherium.*)

Type Loc.—Colorado. Level not ascertained.

Type.—"Lower jaws and entire molar series complete." Yale Univ. Mus.

This species and genus were defined by the presence of *two* lower incisors, while the lower jaw exhibits but *three* premolars on each side. It has an evenly-arched lower border and shallow chin. It remains *indeterminate* until the skull characters become known.

[1] It has unfortunately been injured since it was described and figured by Scott and Osborn, Bull. Mus. Comp. Zoöl., 1887, p. 158.

[2] Contr. Can. Pal., Vol. III, p. 10, Pl. vi, fig. 1.

13. Titanotherium torvum (Cope).

PLATE III.

Symborodon torvus COPE. (Type of genus *Symborodon.*)

SYN. *Symborodon bucco* COPE.

Type Loc.—Colorado. Level not ascertained.

Type.—Complete lower jaws. Coll Am. Mus. Nat. Hist., No. 6365.

Spec. Char.—*Horns* short, above narial opening, ? sub-circular in section; directed forwards, upwards and outwards; no connecting crest. *Nasals* of medium length, notched distally. Zygomatic arches widely projecting with a rounded outer section, slightly flattened vertically. Occiput low, deeply excavated, heavy outer pillars. External premolar cingula reduced or wanting. Dentition: $\frac{2}{0}$, $\frac{1}{1}$, $\frac{4}{3}$, $\frac{3}{3}$.

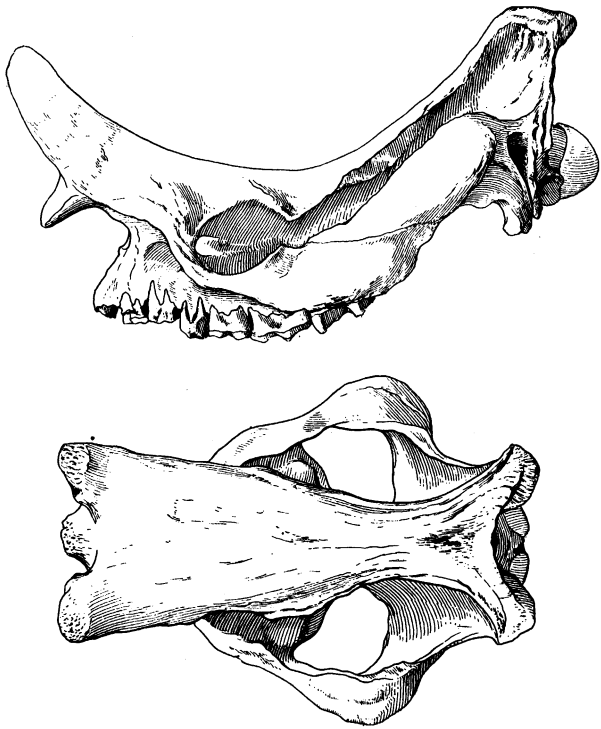


Fig. 2. *Titanotherium torvum* (or *robustum*). Skull (No. 1081) in lateral and superior views. The *nasals* are partly restored.

The type jaw entirely lacks the lower incisors and presents only three premolars upon each side. The premolars exhibit incomplete external cingula. As observed by Cope, it agrees precisely with the lower jaw of Cope's type of *Symborodon bucco* (No. 6345, Am. Mus., Cope Coll.), and it is by combining these two types that we obtain the specific characters given above.

Unfortunately in Cope's type of *S. bucco*, from which all the skull characters in the above definition are derived, the horns and nasals, although present, are very imperfectly preserved. This

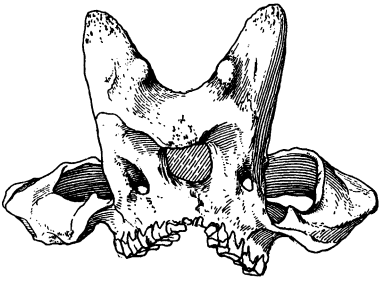


Fig. 3. *Titanotherium torvum* (or *robustum*). Skull (No. 1081) in front view, exhibiting the *branching* of the horns.

makes it impossible to exactly define this species, or determine its sex. The premaxillæ have been lost, so that it is impossible to verify Cope's statement that there are *two* upper incisors.

Cope's associated type of *S. bucco* (Am. Mus., Cope Coll., No. 6346) is the posterior half of a skull with very powerful, rounded, zygomatic arches. It is apparently a male skull, but does not certainly belong to this species.

The most closely related form is Marsh's species *T.* (*Brontops*) *robustum*. It may subsequently prove to be identical. Cope's associated type of *S. bucco* has the same zygomatic arch-section.

14. Titanotherium ophryas (*Cope*).

Symborodon ophryas COPE. (Type of genus *Miobasileus* COPE.)

Type Loc.—Colorado. Level not determined.

Type.—A fragmentary skull, including nasals and horns.

This is practically a *nomen nudum*. The original skull was broken up in removal and transportation, and the original description does not enable us to distinguish the species.

15. Titanotherium acer (*Cope*).

PLATE IV.

Symborodon acer COPE.
SYN. *S. altirostris* COPE. Type, a female skull of *T. acer.*
" *? Menodus syceras* COPE.

Type Loc.—Colorado. Level undetermined.

Type.—A male skull lacking the teeth and zygomatic arches. (Am. Mus., Cope Coll., No. 6348.)

Spec. Char.—*Horns* long, rising on stout maxillary column overhanging narial opening, sub-oval, antero-posterior section of base greater than transverse. ♂ Horns very long, recurved, flattened at summit, with a low connecting crest, and a slight external ridge. ♀ Horns shorter, directed forwards. *Nasals* very short, tapering to extremities. Occiput high and narrow, superior border not incurved. ♀ Zygomatic arch rather slender, slightly spreading. Premolar cingula reduced externally. ♀ Superior incisors vestigial. Lower jaws unknown.

This small species is sharply characterized by the antero-posterior oval form of the horns, the long narrow cranium, and the high slender occiput. The female skull (type of *S. altirostris* Cope, No. 6350, Am. Mus.) has shorter horns but precisely similar skull and nasal dimensions and characters. As in some other female skulls, the connecting crest between the horns is wholly wanting, and the superior incisors have dropped out, although apparently present in the young condition.

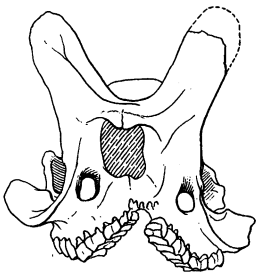


Fig. 3*A*. Skull of female *T.* (*altirostris*) *acer*. (No. 6350), front view.

A second female skull (No. 6349, Am. Mus., Cope Coll.) has horns somewhat flattened posteriorly, but is otherwise similar.

The type of *T. syceras* Cope[1] from the Swift Current Creek, Canada, exhibits horns and nasals of the same character as the above.

As in all the long-horned species examined by the writer, the external premolar cingula are nearly obsolete.

[1] Contr. Can. Pal., III, Pl. viii.

16. Titanotherium heloceras (*Cope*).

PLATE III.

Symborodon heloceras COPE.

Type Loc.—Colorado. Level unknown.

Type.—A skull with teeth, nasals and part of frontals wanting. (No. 6360, Am. Mus., Cope Coll.)

Spec. Char.—*Horns* rudimentary, divergent. Post-glenoid and post-tympanic processes not in contact. *Occiput* broad and low. Zygomatic arches slender, vertical, not spreading.

This animal is very imperfectly known. From the open condition of the external auditory meatus it is evidently a very primitive type. The rudimentary condition of the horns is possibly a female character. The type is of advanced age.

This animal probably had moderately broad, elongate nasals, and three upper and lower incisors. Unfortunately these parts are wanting in the type.

17. Titanotherium bucco (*Cope*).

PLATE III.

Symborodon bucco COPE.

Type Loc.—Colorado. Level unknown.

Type.—A complete skull and lower jaws. Sex unknown. (No. 6345, Am. Mus., Cope Coll.)

This species is a synonym of *T.* (*Symborodon*) *torvum* Cope, as determined by the almost identical characters and measurements of the lower jaws.

18. Titanotherium altirostris (*Cope*).

Symborodon altirostris COPE.

Type Loc.—Colorado. Level unknown.

Type.—A female skull. (No. 6350, Am. Mus., Cope Coll.)

The type of this species is a female skull of the species *T. acer* Cope, described above.

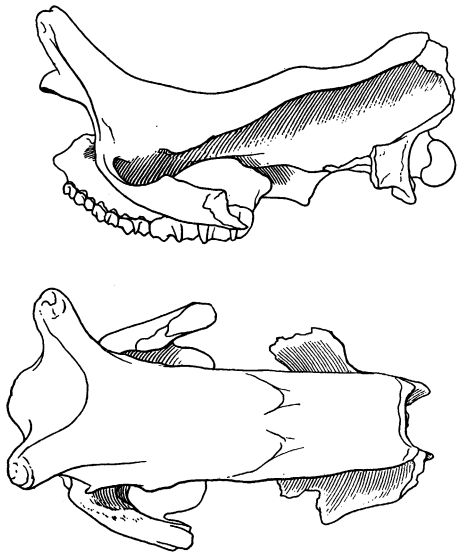


Fig. 4. Skull of female *T.* (*altirostris*) *acer*, side and top views (No. 6350). One-twelfth natural size.

19. Titanotherium trigonoceras (*Cope*).

PLATE III.

Symborodon trigonoceras COPE.

Type Loc.—Colorado. Level undetermined.

Type.—A cranium lacking the teeth. (No. 6355, Am. Mus., Cope Coll.)

Spec. Char.—*Horns* short, rising upon maxillaries, partly over the orbits; ♂ sub-triangular in section at base, directed outwards and upwards, in latest types united by low connecting crest; ♀ more slender and rounded superiorly, no connecting crest. *Nasals* very long, overhanging symphysis, square or broadening distally, notched. Zygomatic arch vertically deep in section, with an inferior lateral bulge in front of glenoid facet. Occiput low and broad, incurved upon superior border; ♂ robust lateral pillars. Incisors vestigial. Canines moderately large. Premolars with external and internal cingula. Dentition: $\frac{2-0}{}$, $\frac{1}{}$, $\frac{4}{}$, $\frac{3}{}$. Lower jaw unknown.

The type skull lacks most of the teeth. The associated type (Am. Mus., Cope Coll., No. 6356) exhibit four vestigial incisors. As observed by Cope,[1] it is of smaller size, substantially of the

[1] Bull. U. S. Geol. Surv. Terrs., 1873, p. 490. (Pub. 1874.)

same proportions and characters as *T.* (*Brontotherium*) *ingens* Marsh, but the latter is a distinct species. The last upper molar has quite a distinct second internal cone. The 'connecting crest' is feebly developed.

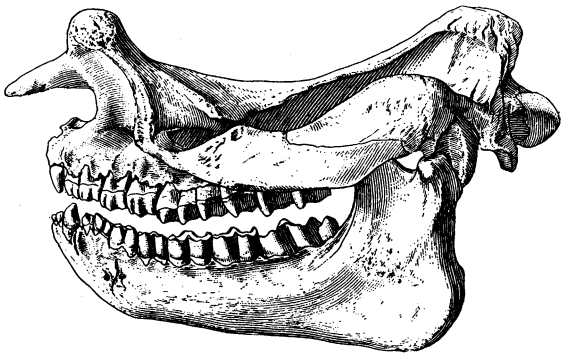


Fig. 5. *Titanotherium trigonoceras.* Skull (No. 1445) and lower jaws (No 516), found in the lower beds. One-tenth natural size.

Two fine skulls (Nos. 501, 1445) in the American Museum Collection are provisionally referred to this species, although the horns are less distinctly triangular, presenting a transition between *T. coloradense* and *T. trigonoceras.*

In No. 501 there are two upper incisors and no second internal cone upon the last upper molar. In the closely similar No. 1445 there are no evidences of upper incisors, and there is a decided second internal cone upon the last upper molar.

In other respects the two skulls agree quite closely. The 'connecting crest' is feebly developed, thus the horn section is a longitudinal oval with a triquetrous base. The nasals are long and expand somewhat distally. The occiputs are robust and somewhat indented superiorly. The post-glenoid and post-tympanic processes are in slight contact.

This species, characteristic of the lower beds and lower portion of the middle beds, is sharply defined. It is probably ancestral to *T. ingens* Marsh, which is confined to the middle beds and may be distinguished by the long pointed canines and very large size.

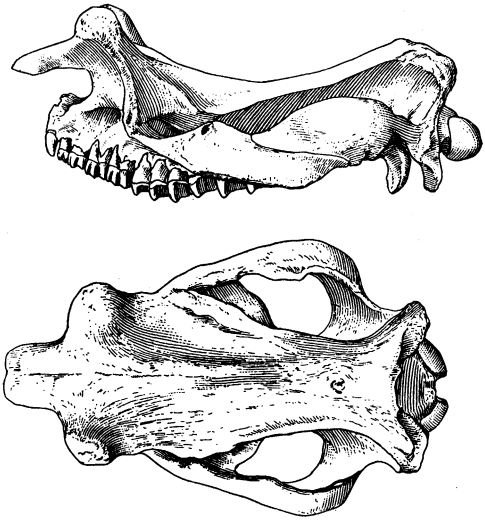


Fig. 6. *Titanotherium trigonoceras.* Skull (No. 1445), superior view. Skull (No. 501), in side view. One-twelfth natural size.

20. Titanotherium ingens (*Marsh*).

PLATE III.

Brontotherium ingens MARSH.

Type Loc.—

Type.—A complete male skull. Yale Univ. Mus.

Spec. Char.—*Horns* short, rising upon maxillaries partly above orbits; ♂ sub-triangular in section, with 'connecting crest'; directed strongly upwards and outwards. ♀ more slender, elongate oval in form, no 'connecting crest.' Nasals in both sexes, long, expanding and rugose distally, notched. Zygomatic arch with a deep vertical section, and a decided bulge just in front of glenoid facet, strongest in ♂ skulls. Incisors ? 2–0, vestigial or wanting. Canines very long and pointed, extending below level of premolars, ♂ robust, ♀ slender. Premolars and molars with robust external and internal cingula. Second internal cone of last upper molar variable, sometimes strongly distinct. Dentition: $\frac{2}{2}-\frac{0}{0}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{3}{3}$.

The four fine skulls (Nos. 505, 506, 1066, 1067) in the American Museum Collection are referred to this species, although in all of them *the upper incisors are vestigial or wanting.* Marsh assigns two upper incisors to his type, but the premaxillaries are apparently wanting.

Two of these skulls (Nos. 506, 1067) are apparently females, the horns are more slender and pointed; the upper and lower canines are long but less robust. Neither skull has any trace of upper or lower incisors.

Of the supposed male skulls No. 505 agrees exactly with Marsh's type specimen; the outer upper incisor is represented by one small alveolus, the tooth has disappeared. The other skull, No. 1066, has *two* vestigial alveoli. It is apparent that in this species, so closely related to *T. trigonoceras*, the *upper incisors are variable, vestigial or wanting*.

These two male skulls have strong canines, more robust zygomatic arches, and strong 'connecting crests' between the very stout triangular horns.

We can readily distinguish this species by the vigorous development of the canine, premolar and molar teeth, which far surpass in size and in the development of cingula those of any other type. (See measurements, Table II.)

Vertical or lateral crushing greatly alters the angles and appearance of the horns. Skull No. 1066 is vertically crushed, and thus closely resembles the type of *Menops varians* Marsh.

21. Titanotherium hypoceras (*Cope*).

Symborodon hypoceras COPE.

Type Loc.—Colorado. Level unknown.

Type.—A fragmentary cranium, parts of nasals, maxillaries, frontals, etc. (Am. Mus. Nat. Hist., Cope Coll., No. 6361.)

This species is indeterminate, owing to the fractured condition of the type. The horns resemble those of a young individual, or of a female skull.

22. Titanotherium montanum (*Marsh*).

Anisacodon montanus MARSH, Am. Jour. Sci. 1875, p. 245.
? SYN. *T. elatum* MARSH.
Diconodon (non-*Anisacodon*) MARSH, Am. Jour. Sci. 1876, p. 339.

Type Loc.—Not published.

Type.—A fragmentary skull, including the maxillaries. The chief character assigned to distinguish this genus and species is the large second internal cone

upon the last upper molar ; this character is of very doubtful taxonomic importance, since this cone is a variable character, as we have seen above in *T. trigonoceras* and *T. ingens.* The dentition assigned by Marsh is: $\frac{0}{1}$, $\frac{1}{1}$, $\frac{4}{3}$, $\frac{3}{3}$.

The skull referred to this species by Marsh, in the National Museum Collection, resembles a female skull of *T. elatum ;* the horns of transverse oval section are short, placed above the nares, directed forwards and united at the base by a strong connecting crest.

24. Titanotherium angustigenis (*Cope*).

Menodus angustigenis COPE, Ann. Rep. Geol. Surv. Canada, 1886, C. p. 81.
Haplacodon angustigenis COPE, Am. Nat. March, 1889, p. 153.

Type Loc.—White River Beds of Swift Current Creek, Canada.

Type.—Two maxillary bones. Assoc. type : Two lower jaws.

The characters of the type do not enable us to define this species satisfactorily. The *associated* type is readily distinguished by the extreme narrowing of the *symphysis mandibuli.* The type is interesting as exhibiting three premolars upon one side and two upon the other, and demonstrating the variability of these teeth. The genus *Haplacodon* has not been retained by its author.

25. Titanotherium tichoceras (*Scott & Osborn*).

PLATE III.

Menodus tichoceras S. & O. Bull. Mus. Comp. Zoöl. Aug. 1887, p. 157.

Type Loc.—South Dakota. Level unknown.

Type.—A skull and teeth ; horns partly broken. Coll. Harv. Univ. Mus.

Spec. Char.—*Horns* sub-triangular to cylindrical in section, rising between orbits and nares, inclined forwards and outwards ; not united by connecting crest. *Nasals* of medium length, slightly tapering. Zygomatic arch deep, with a bulge opposite glenoid facet. Occiput unknown. Two superior incisors. Premolars without external cingulum ; internal cingulum reduced or obsolete. Dentition : $\frac{2}{}$, $\frac{1}{}$, $\frac{4}{}$, $\frac{3}{}$.

This species is clearly distinguished from the *T. trigonoceras* and *T. ingens* type by the decidedly more anterior position and

more rounded section of the horns, by the correspondingly shorter nasals, and by the absence of external cingulum upon the premolars. It resembles these species closely in the form of the zygomatic arch. The sex of the type is uncertain; the rather large canines indicate that it is a male skull. It might be considered a female skull of *T. dolichoceras* but for the longer nasals and wholly different horn-section.

26. Titanotherium dolichoceras (*Scott & Osborn*).

PLATE IV.

Menodus dolichoceras S. & O. Bull. Mus. Comp. Zoöl. Vol. XIII, Aug. 1887, p. 158.

Type Loc.—South Dakota. Level unknown.

Type.—A male skull, lacking dentition and zygomatic arches. Coll. Harv. Univ. Mus.

Spec. Char.— ♂ *Horns* long, placed above nares, forwards and outwards, with an oval section placed obliquely to the longitudinal axis of the skull; no connecting crest. *Nasals* very short, tapering. Occiput not very broad. Premolars with reduced external cingulum.

The horns in this species are placed as in *T. robustum*, but the oval section is oblique instead of transverse, and the nasals are much shorter. This position and section of the horns is highly characteristic. A close approach to it is found in the type of *T.* (*Allops*) *serotinus* Marsh, which may prove to be a female skull of *T. dolichoceras*. The sections are shown in Diagram II.

27. Titanotherium platyceras (*Scott & Osborn*).

PLATE IV.

Menodus platyceras S. & O. Bull. Mus. Comp. Zoöl. Vol. XIII, Aug. 1887, p. 158.

Type Loc.—South Dakota. Upper Titanotherium Beds.

Type.— ♂ A pair of horns. Nasals imperfect. Coll. Harv. Univ. Mus. Assoc. type, Coll. Am. Mus., No. 1448.

Spec. Char.— ♂ *Horns* placed vertically in front of symphysis, extremely flattened transversely, directed forwards, upwards, and slightly recurved; united by a deep connecting crest; rugose at extremities, with an external ridge extend-

ing towards malars. *Nasals* extremely short, deeply notched. Zygomatic arches expanding into two broad flattened rugose plates. Occiput low, deeply indented, with stout lateral pillars. External auditory meatus enclosed by deep union of post-glenoid and post-tympanic. Canines stout, obtuse. Two pairs of upper incisors. Premolars with obsolete external cingulum. ♂ Dentition: $\frac{2}{2}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$.

Fig. 7. *Titanotherium platyceras.* Skull (No. 1448), in lateral view. The occipital region is composed of fragments placed together in plaster. One-tenth natural size.

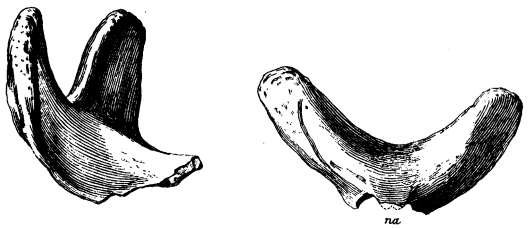


Fig. 7*A*. *Titanotherium platyceras.* Type. Horns and fragmentary nasals. Harv. Univ. Mus.

The characters originally assigned to this species from the type horns in the Harvard University Museum are now reinforced by a superb male skull in the American Museum Collection (No. 1448). It apparently represents the very latest stage of development of the Titanotheres before their sudden extinction. The extreme anterior position of the horns, their flattened section, the deep connecting crest, the vestigial nasals, the great zygomatic plates, the deeply excavated occiput—all are in a terminal phase beyond which further specialization seems impossible. At the

same time it is noteworthy that in this skull both the incisors are retained and the last molar shows only a slight distinctness of the second cone, indicating that this character is not essentially a progressive one. The premolar cingula are markedly reduced. The horn sections are shown in Diagram I. The figures of the skull are inaccurate in not clearly indicating that the posterior part of the cranium is largely fragmentary and restored.

28. Titanotherium robustum (*Marsh*).

Brontops robustus MARSH.

Type Loc.—Upper Titanotherium Beds.

Type.—A perfect skull and nearly complete skeleton. Coll. Yale Univ. Mus.

Spec. Char.—*Horns* placed anteriorly, above nares, directed forwards and outwards, transverse oval in section, no connecting crest. *Nasals* somewhat below medium length, slightly tapering or nearly square distally. Zygomatic arch with a strong outward projection, rounded in outer section. Premolars with reduced external cingula. Dentition : $\frac{2}{1}$, $\frac{1}{1}$, $\frac{4}{3}$, $\frac{3}{3}$.

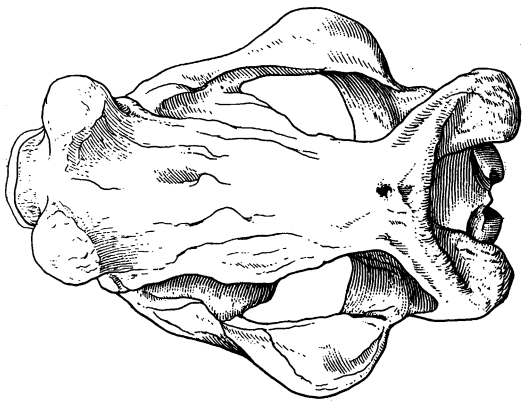


Fig. 8. *Titanotherium robustum.* Skull (No. 1069), in superior view. One-twelfth natural size.

Marsh's type is a superb skull and jaws and nearly complete skeleton, which was figured and fully described in 1889.[1] This

[1] Am. Jour. Sci., Feb., 1889, p. 163, Pl. vi.

animal approaches *T. torvum* Cope, but appears to differ specifically in the stronger transverse oval of the horns (compare sections in Diagram II), and in the less extensive outward arching of the zygomata. In *T. torvum* the expansion of the arch is somewhat flattened vertically ; in *T. robustum* the swelling is vertically rounded (as in Cope's associated type). These differences, however, may subsequently be found not to possess specific value.

Two fine skulls in the American Museum Collection (Nos. 1069, 1083) apparently belong to this species, although the nasals are somewhat longer and more quadrate distally. They exhibit the same transverse oval horn section, two strong upper incisors, the alveoli of powerful canines, the absence of a connecting crest between the horns.

Judging by the large upper canines, Marsh's type is the skeleton of a male, the sexual characters of this species have yet to be determined. Some light is thrown upon this by No. 508.

The skull and nearly complete skeleton (508) in the American Museum have already been described as a *female* of this species in a previous number of the Bulletin. Unfortunately the canines and alveolar borders of the incisors are wanting, depriving us of these characters so distinctive of sex. The horns are feebler, and the zygomatic arches are much less expanded than in Marsh's type, indicating that this is a female animal.

29. Titanotherium dispar (*Marsh*).

Brontops dispar MARSH, Am. Jour. Sci. 1887, pp. 327, 329.

Type Loc.—South Dakota Titanotherium Beds.

Type.—A nearly complete skull with lower jaws and entire dentition. Coll. U. S. Geol. Surv.

This species has not as yet been defined in such a manner that its position can be determined.

30. Titanotherium varians (*Marsh*).

PLATE III.

Menops varians MARSH, Am. Jour. Sci. 1887, p. 328.

Type Loc.—South Dakota. Titanotherium Beds.

Type.—"Skull of a large adult male."

Marsh has distinguished this species by the formula $\frac{2}{}, \frac{1}{}, \frac{4}{}, \frac{3}{}$. The horns are directed outwards and subtriangular in section, and the connecting crest is very low. The nasals are elongate, spreading, and notched distally.

We cannot, from the characters given, clearly distinguish this species from *T. trigonoceras* or *T. ingens*, to which it is apparently related.

31. Titanotherium curtum (*Marsh*).

PLATE IV.

Titanops curtus MARSH. (Type of Genus *Titanops.*)

Type Loc.—Colorado. Probably Upper Titanotherium Beds.

Type.—A complete male skull, with imperfect premaxillaries.

Spec. Char.— ♂ *Horns* placed above narial opening, transverse flattened oval section, directed upwards, outwards and forwards, with an external crest to malars and a strong connecting crest. *Nasals* extremely reduced. Zygomatic arches moderately expanded. Canines powerful.

This species is intermediate between *T. elatum* and *T. ramosum*. The horn section is similar to that in *T. elatum*, but the nasals are very much more abbreviated.

32. Titanotherium elatum (*Marsh*).

PLATE IV.

Titanops elatus MARSH.

?SYN. *Diploclonus amplus* MARSH.

Type Loc.—South Dakota. Upper Titanotherium Beds.

Type.—A male skull lacking zygomatic arches.

Spec. Char.—*Horns* placed above anterior nares and symphysis; directed forwards, upwards and outwards; transverse oval (flattened posteriorly) in sec-

tion ; united by connecting crest. ♂ Horns elongate, vertical and recurved, rounded at tip ; a strong external ridge to malars ; deep connecting crest. ♀ Horns short, projecting forwards, pointed, rugose, or imperfectly ossified at tips, connecting crest less prominent or wanting. *Nasals* ♂ ♀ rather narrow and short, tapering, somewhat variable in length and size, notched distally. Zygomatic arch spreading ♂ with broad, vertically-compressed plates ; ♀ with a stout rounded projection. Occiput low and broad, ♂ with powerful lateral crests, ♀ with moderate lateral crests. Incisors, ♂ 2-1, ♀ variable 2-0. Canines short, obtuse, ♂ powerful, ♀ small, feeble.

Marsh's type is an imperfect male skull which he has briefly characterized.

The above definition is from an exceptionally fine male skull (No. 492, Am. Mus. Coll.), and from a less complete male skull and perfect pair of jaws (No. 1070, Am. Mus. Coll.). These are apparently identical with Marsh's type. The *female* characters

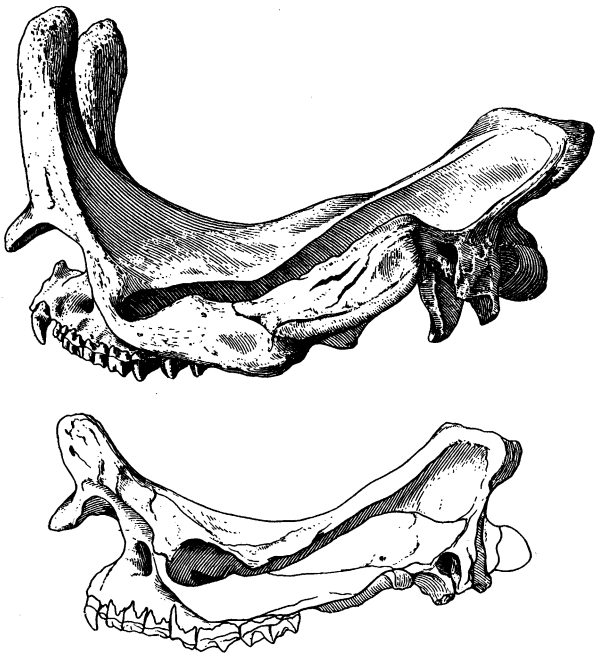


Fig. 9. *Titanotherium elatum.* Male (No. 492) and female (No. 1006) skulls, contrasted in lateral view. One-twelfth natural size.

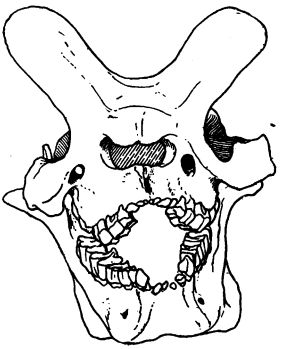


Fig. 10. *Titanotherium elatum.* Skull and jaws (No. 1070), in front view. One-twelfth natural size.

are taken from four smaller skulls found in the same geological level, distinguished by a rusty-brown color. In these skulls the horns are much shorter but have the same section, position and strong connecting crest, and it is highly probable that they are females of *T. elatum.* If this conclusion is correct we derive from these skulls a number of very important facts.

Both *male* skulls (492, 1070) exhibit a strong pair of upper incisors. The lower jaw of 1070 exhibits two lower incisors. No. 492 is characterized by short robust canines, very long recurved horns, massive zygomatic arches, extending into flattened plates, a robust deeply incurved occiput, small but well-formed nasals.

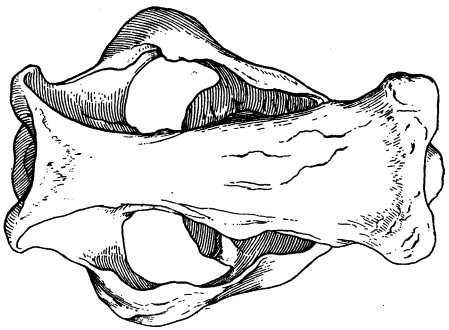


Fig. 11. *Titanotherium elatum.* Female skull (No. 1005), superior view. One-twelfth natural size.

In the supposed *female* skulls we find less perfect nasals, short horns, strong connecting crests, less expanded zygomata, feeble canines and extremely variable incisors.

In No. 1005, a small female skull, there are no upper incisors.

In No. 1006, a somewhat larger female skull, there is one small upper incisor upon each side.

In No. 1008, otherwise closely similar to the above skulls and found in the same level, there is also one small upper incisor upon each side, the horns are pointed (instead of rounded or obtuse as in Nos. 1005, 1006), and exhibit rugose projections upon the inner side about one-third from the base. This specimen agrees very closely with the type of *T.* (*Diploclonus*) *amplum* Marsh.

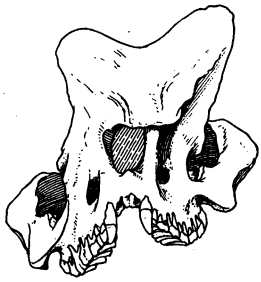


Fig. 12. Skull of female *T. elatum* (No. 1006). One-twelfth natural size.

LOWER JAWS.

The very large pair of lower jaws (No. 1051) may be provisionally referred to this species, although the dental series is longer than in the male skull No. 492. They exhibit short, robust canines, two stout incisors, premolars without external cingula. The large mental foramen opens directly below the third premolar.

33. Titanotherium serotinum (*Marsh*).

Allops serotinus MARSH.

Type Loc.—South Dakota. Level not published.

Type.—A skull.

Marsh distinguishes this species by the dental formula $\frac{1}{1}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$. It has not yet been figured or defined. An examination of the

type specimen indicates that skull No. 520, in the American Museum, is very similar. This in turn is most closely related to *T. dolichoceras.* This skull has small outer incisors only. The horns have no 'connecting crest'; they diverge widely and have an oval section, obliquely placed. The nasals are short and deeply notched; the zygomatic arches are moderately expanded. The summit of the occiput is more deeply incurved than in the type of *T. dolichoceras.*

35. Titanotherium selwynianus (*Cope*).

Menodus selwynianus COPE, Am. Nat. 1889, p. 628.

Type Loc.—Swift Current Creek, Canada.

Type.—Nasals detached from skull.

Spec. Char.—*Nasals* prominent, narrow and vaulted, lateral borders nearly parallel, extremities rounded.

This species is very imperfectly known. As described by Cope,[1] it appears to be a primitive and distinct species.

36. Titanotherium syceras (*Cope*).

Menodus syceras COPE, Am. Nat. 1889, p. 628.

Type Loc.—Swift Current Creek, Canada.

Type.—Coössified nasals with horns.

The type of this species resembles very closely the female nasals and horns of *Titanotherium acer* Cope.

37. Titanotherium amplum (*Marsh*).

Diploclonus amplus MARSH, Am. Jour. Sci. 1890, p. 523.

Type Loc.—Not published.

Type.—"A nearly complete skull."

Spec. Char.—*Horns* high, compressed transversely with a strong connecting crest; a prominent knob upon inner superior margin; an external ridge. *Nasals* projecting very little. Zygomatic arches widely expanded. Last upper molar with two cones. ? Two upper incisors.

[1] The nasals are figured in Pl. V, Figs. 3, 3*a*, 3*b*, Contr. Can. Pal., Vol. III, p. 17.

The above definition is from the author's description. The internal knob appears to be an *individual variation* rather than a specific or generic character. As above noted it appears in our collection in a skull which is probably a female of *T. elatum*, yet closely similar to Marsh's type of *T. amplum*. This knob is also seen in the horns of skull No. 1081 of our collection, which we provisionally refer to *T. torvum*.

38. Titanotherium avum (*Marsh*).

Teleodus avus MARSH, Am. Jour. Sci. 1890, p. 524.

Type Loc.—Not published.

Type.—Not stated. Characters assigned in lower jaw.

This species is characterized by the presence of three lower incisors in each jaw. The type has but three lower premolars. Hatcher believes that this species possesses a trapezium.

This character and the presence of three lower incisors unites this genus with *Diplacodon*.

39. Titanotherium ramosum, sp. nov.

PLATE IV.

Type. Loc.—Upper Titanotherium Beds. South Dakota.

Type.—A complete male skull, lacking incisor border. (No. 1447, Am. Mus. Nat. Hist.)

Spec. Char.—♂ *Horns* placed above symphysis, greatly expanded at the summits, section plano-convex ; a strong 'connecting crest,' *Nasals* extremely short. Zygomatic arches expanded into two wide flat plates. Incisors and canines unknown. Premolars with reduced external cingula.

The distal spreading or branching of the horns is the character by which this species is designated. It differs from *T. elatum* in this character, but more especially in the great depth of the 'connecting crest' and the extreme flattening of the horns, the section as shown in Diagram I, being intermediate between that of *T. elatum* and of *T. platyceras*. It is remarkable that the teeth in this large skull are relatively of small size; the last upper molar has no second cone.

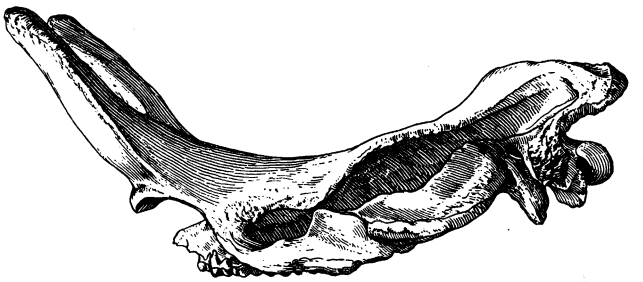


Fig. 13. *Titanotherium ramosum.* Type skull (No. 1447), in lateral view. One-twelfth natural size.

Found near this skull was a pair of lower jaws (No. 1449) containing teeth of lesser longitudinal measurement. The chin is very shallow. There are two robust incisors upon each side; the canines are short and obtuse; the premolars lack the external cingula. The formula is $\frac{2}{2}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$.

Characters of Lower Jaws.

It is not possible to satisfactorily determine the specific characters of the lower jaws from the materials at our disposal.

No. 516.—This is a fine pair of small jaws from the lower beds with a formula $\frac{2}{2}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$. The dental series is of exactly the same size as in skulls Nos. 501 and 1445, indicating that these jaws belong to *T. trigonoceras*, but the incisors are much more strongly developed than in any of the known skulls of this species.

Nos. 1067, 506.—These jaws are both associated with female skulls of *T. ingens*. The rami are long and deep, with a full well-rounded chin. No lower incisors; strong cingula.

Nos. 6345, 6365.—These jaws, belonging to *T. torvum*, are much shorter and shallower than in *T. ingens*. No lower incisors; feeble external cingula.

Nos. 1052, 508.—These jaws, belonging probably to *T. robustum*, are distinguished by the very large size of the mental foramen, which is placed beneath the line between the third and fourth premolars. Canines stout in male (1052). Cingula feeble.

TABLE III.—DIVISION OF THE TITANOTHERIUM BEDS, AND VERTICAL DISTRIBUTION OF SPECIES.

	WHITE RIVER BEDS, COMPOSITE SECTION, OLIGOCENE.	CHARACTERISTIC SPECIES.
TOTAL THICKNESS, 180 FEET. Upper Beds, 80.	Titanotheres of large and medium size. Males with horns 8 to 17 inches in length, placed above nares, transverse oval or flattened in section, usually a connecting crest. Nasals pointed, medium or short. Premolars with reduced cingula. Incisors 2–0. External auditory meatus deeply enclosed.	*T. platyceras*, 1448. *T. ramosum*, 1447. *T. elatum*, 492. *T. robustum*, 518.
Middle Beds, 100.	Titanotheres of large and medium size. Males with horns 7 to 9 inches in length, placed above maxillaries, oval or triangular in section; sometimes a connecting crest. Nasals long, quadrate. Incisors 2–0. Premolar cingula varying. External auditory meatus always closed below.	**T. tichoceras*. *T. ingens*, 505. **T. trigonoceras*.
Lower Beds, 50.	Titanotheres of medium and small size. Horns from 4 to 6 inches in length, placed above maxillaries, antero-posterior oval to sub-triangular section, no connecting crest. Nasals long. Incisors 3–0. Premolar cingula varying. External auditory meatus sometimes closed below.	*T. trigonoceras*, 501. *T. coloradense*. **T. heloceras*, 6360.

No. 1051.—This jaw of unusual size is provisionally referred to *T. elatum*. The lower border reaches an angle below the fourth premolar, and in front of this extends upwards into a shallow chin. Cingula upon premolars feeble.

Nos. 1061 and 1068 represent the latest type of jaw, belonging either to *T. elatum* or *T. ramosum*. As in the above (No. 1051) the chin tapers rapidly upwards from a point below the fourth premolar. Cingula feeble.

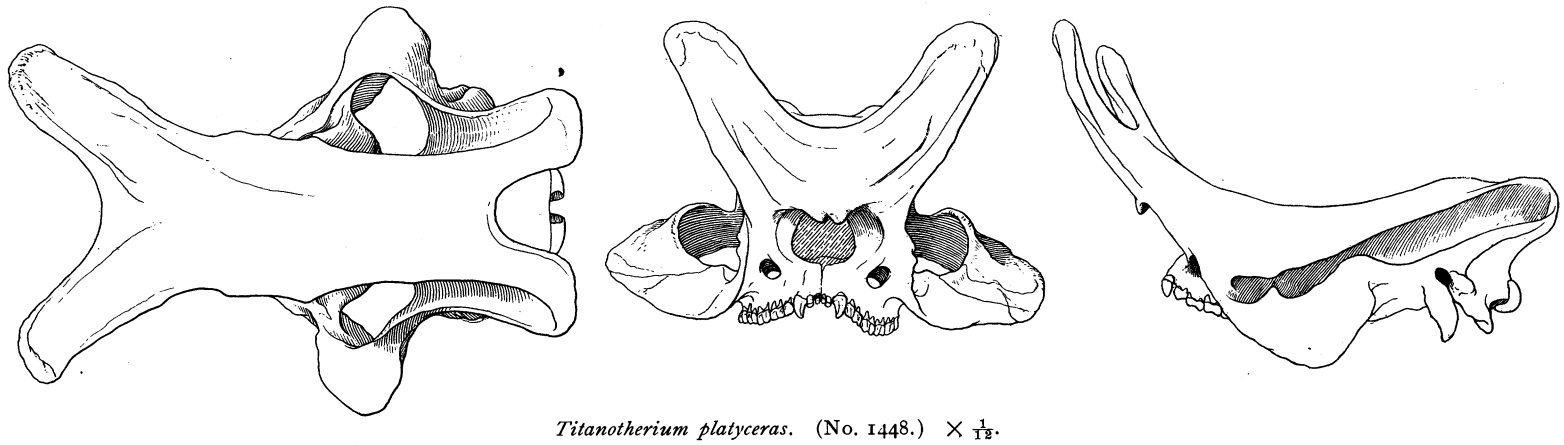
III.—Distribution.

The relation of the evolution of the Titanotheres to the geological levels was first clearly pointed out in an important article by Hatcher.[1] The above table is his, with some modifications and the addition of the specific forms characteristic of the various beds so far as they are known. The geological level of the species marked with a * is still a matter of inference, not of record.

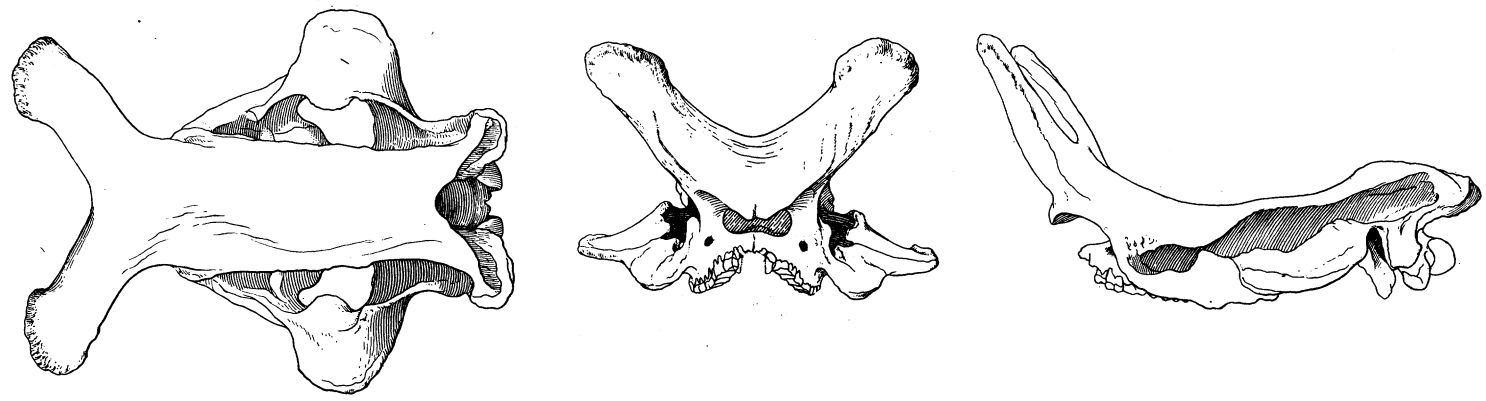
It is true that the above inductions as to growth, sexual and variable characters require confirmation by the examination of a very large number of skulls. In general they are probably correct. They indicate that the principles of generic and specific division adopted by Cope, and in a large degree by Marsh, are wholly untenable—for the strict application of these principles would multiply genera and species *ad infinitum*.

The phylogeny of the species is still so obscure that it is rash to speculate about it.

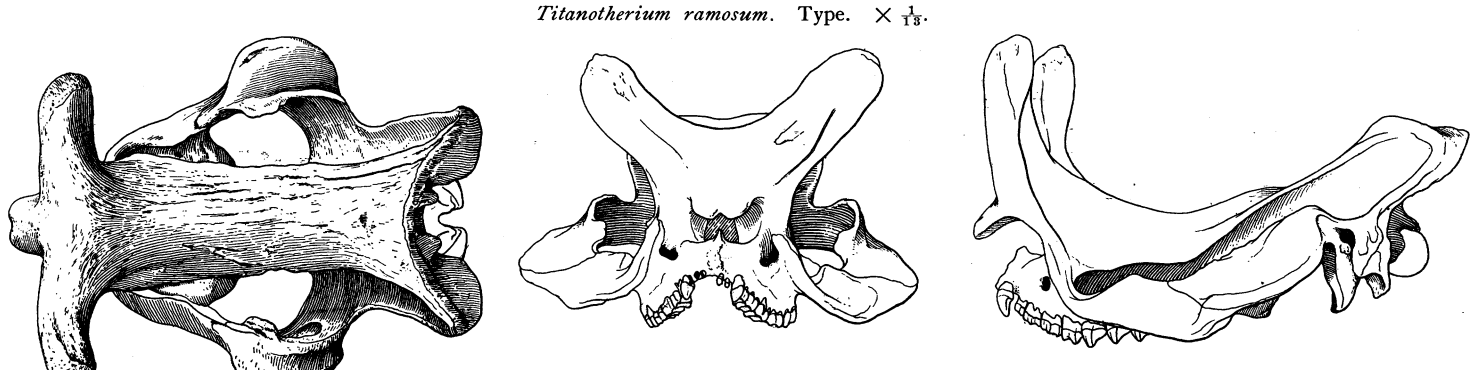
[1] 'The Titanotherium Beds,' American Naturalist, March, 1893, p. 204.



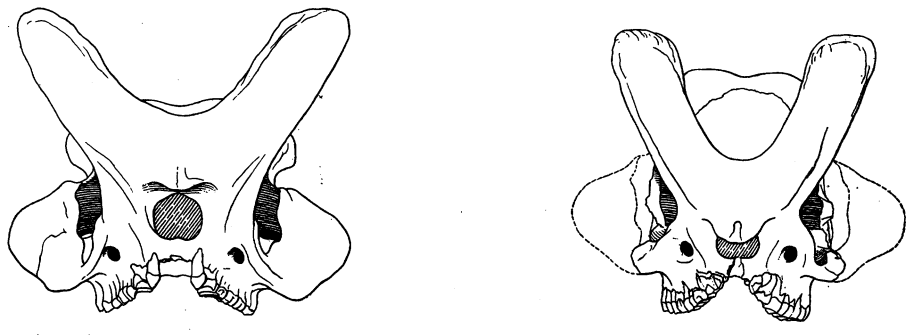
Titanotherium platyceras. (No. 1448.) × $\frac{1}{12}$.



Titanotherium ramosum. Type. × $\frac{1}{18}$.

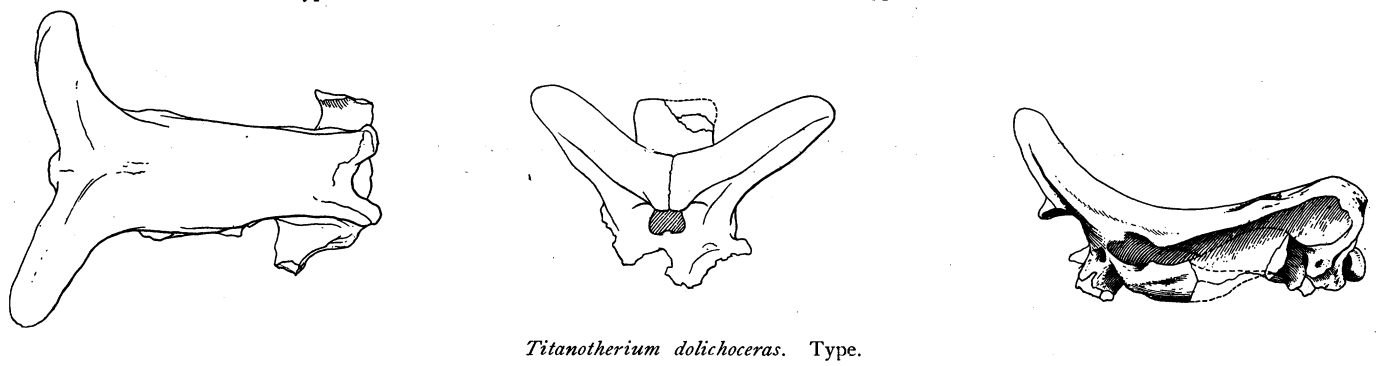


Titanotherium elatum. (No. 492.) × $\frac{1}{15}$.

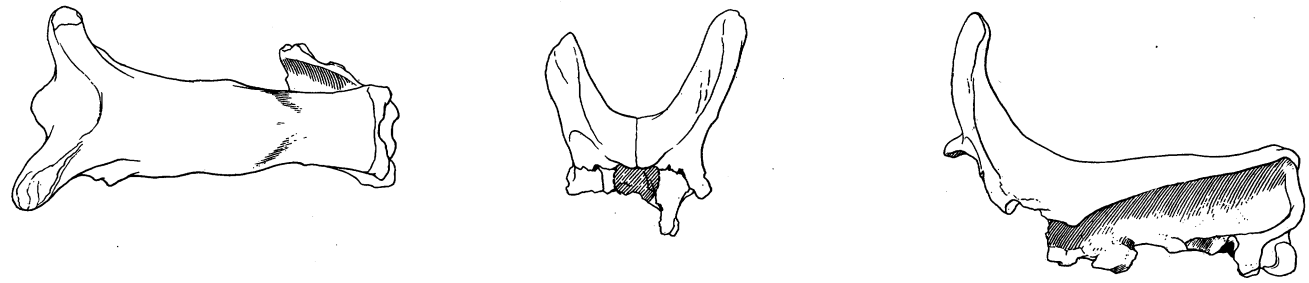


Titanotherium curtum. Type.

Titanotherium elatum. Type.



Titanotherium dolichoceras. Type.

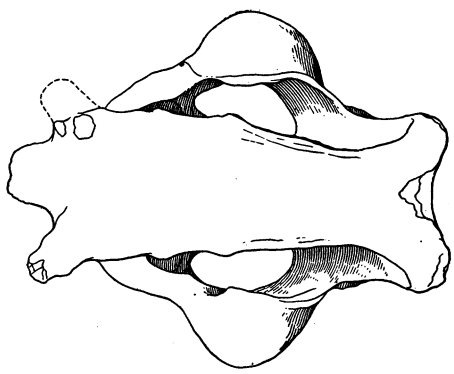


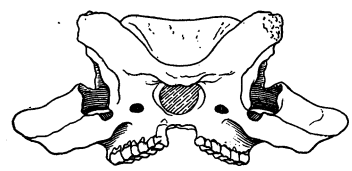
Titanotherium acer. Type. × $\frac{1}{14}$.

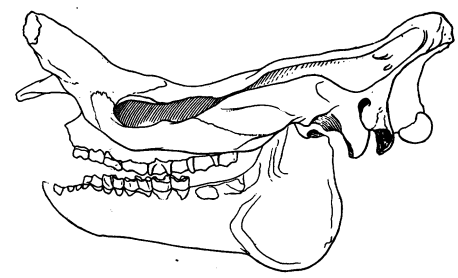
Superior View. Anterior View. Lateral View.

The Long-Horned Titanotheres.

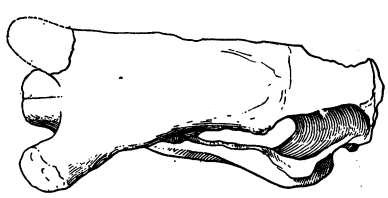
All figures (excepting *T. dolichoceras*) reduced to the same scale. About one-fourteenth natural size.

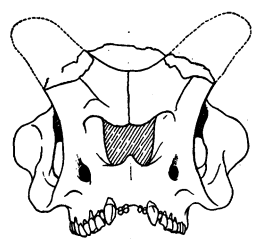


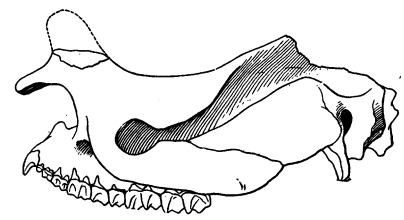




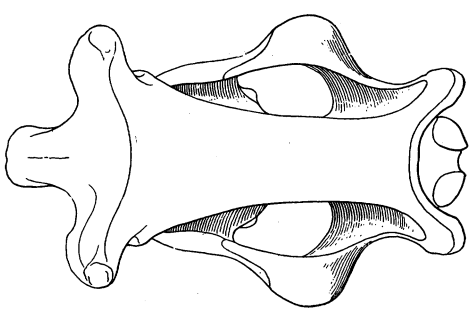
Titanotherium bucco. Type. × $\frac{1}{14}$.

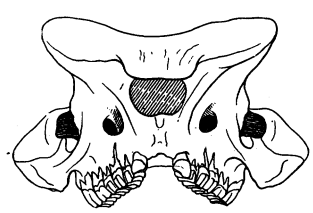


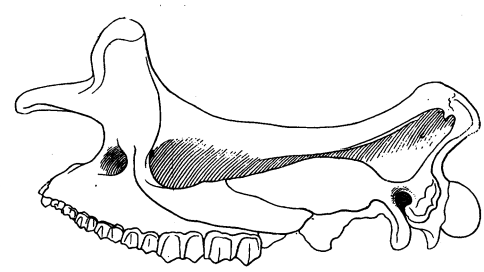




Titanotherium tichoceras. Type.



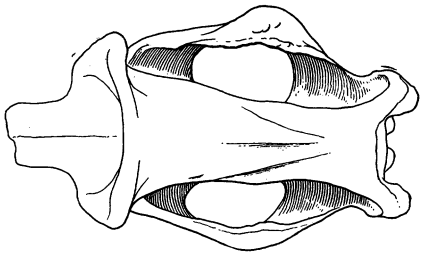


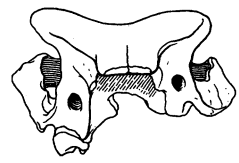


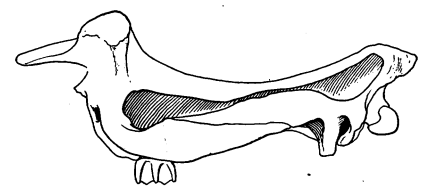
T. ingens. Type. × $\frac{1}{15}$.

T. (varians). Type.

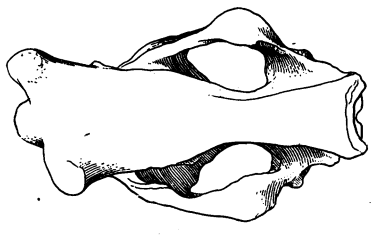
T. ingens. Type.

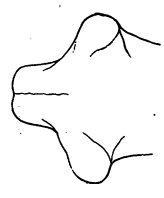


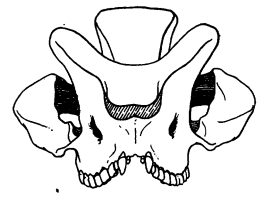


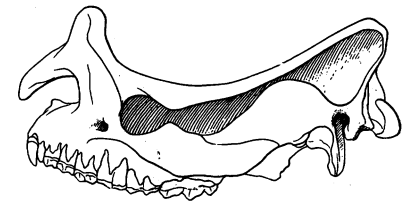


Titanotherium trigonoceras. Type. × $\frac{1}{14}$.

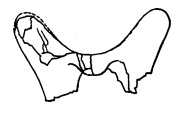


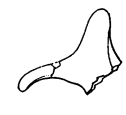




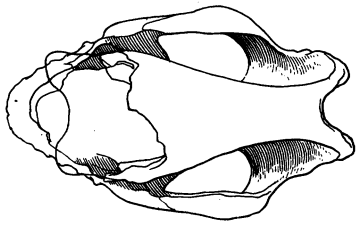


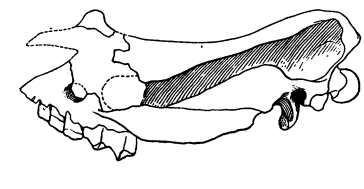
Titanotherium coloradense. (Harv. Univ. Museum.)





Titanotherium coloradense. Type.





Titanoceras heloceras. Type. × $\frac{1}{16}$.

SUPERIOR VIEW. ANTERIOR VIEW. LATERAL VIEW.

THE SHORT-HORNED TITANOTHERES.

All figures reduced to the same scale. About one-fourteenth natural size.