Further Notes on the Gigantic Extinct Rhinoceros, Baluchitherium, from the Oligocene of Mongolia

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Article I.—FURTHER NOTES ON THE GIGANTIC EXTINCT RHINOCEROS, *BALUCHITHERIUM*, FROM THE OLIGOCENE OF MONGOLIA[1]

BY WALTER GRANGER AND WILLIAM K. GREGORY

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The present article is designed to extend and supplement the results set forth in Novitates No. 78, 1923, by the late Henry Fairfield Osborn and to describe the "*Baluchitherium*" material obtained in the Baron Sog and Houldjin beds of Oligocene age by the Central Asiatic Expeditions in 1922–1930. While nothing like complete associated skeletons was found, there were enough partial associations of limb bones with vertebrae or jaws to justify a revised "paper restoration" of the skeleton of this animal, together with notes on its relationships and chief structural features. Our new restoration (Fig. 47) was first published in very brief articles in Novitates (April 1, 1935) and Natural History (April, 1935).

[1] Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution number 135.

SKULL

It has already been remarked by Osborn (1923) that "the skull o *Baluchitherium grangeri*, while of enormous size . . . is relatively primi tive in structure," and that "this is a primitive Eocene and Lowe Oligocene form of skull grown large." In this connection it is also note worthy that the pair of downwardly directed upper incisors in coöpera tion with the forwardly directed pair of conical lower incisors, have ever appearance of being homologous with the corresponding teeth in *Trigo nias osborni* and therefore of representing i^2 and i_1, respectively.

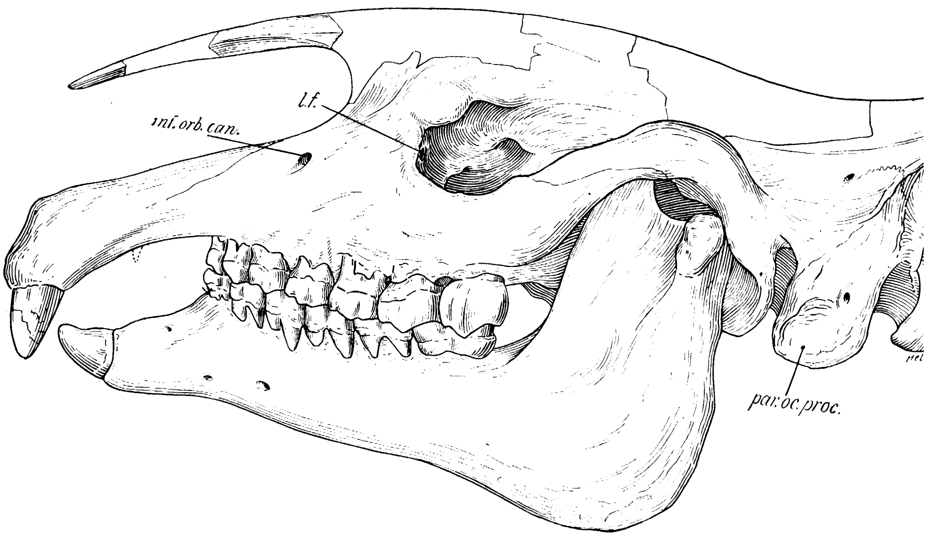


Fig. 1. *Baluchitherium grangeri* Osborn. Type skull. Amer. Mus. No. 1865($\times {}^1/_{10}$ natural size.

Osborn (1923, p. 6) has also suggested that the enlarged upper inci sors functioned as defensive tusks; we feel, however, that their primar function was to assist in the sudden jerking loose of shrubs by downwar movements of the head and neck, since they are well placed to act thu as picks and levers, while the skull (Fig. 1) is braced to resist such stresse through its strong rostrum, down-curved zygomata and greatly empha sized basi-occipital eminence.

The cheek teeth (Fig. 2) are also of primitive rhinoceros type, bu slightly hypsodont and frequently well worn. They are rather small fo such huge animals, so that the food was probably not very silicious

Close relationships on the one hand with Cooper's *Paraceratherium* and on the other with Borissiak's *Indricotherium* are indicated (see page 54 below).

In general the skull of *Baluchitherium* is remarkable for its great length and dorso-ventral lowness; while its occiput (Fig. 3) above the condyles is extremely narrow as compared with that of the titanotheres or even of recent rhinoceroses. This contrast is associated with the absence of horns at the front end of the head, the use of which, especially in the titanotheres, generated enormous oblique stresses on the occiput and necessitated a huge development of lateral crests to withstand the pull of the immensely thick neck muscles. In *Baluchitherium*, on the contrary, the occipital muscles although doubtless very strong were extended vertically rather than transversely. Near the upper border of the occiput there was a very large and deep median pit for the ligamentum nuchae. Thus the skull seems to have been normally suspended from above and, as will presently be shown, the characters of the neck vertebrae do not suggest to us that the animal normally held its head above its back or that it browsed on branches above its head.

While the occiput itself is very narrow, the occipital condyles are extremely wide. The huge size of the paroccipital processes of the exoccipital in *Baluchitherium* implies great strength of the cephalo-humeral muscles. The channel for the ventral muscles of the neck on the under sides of the cervical vertebrae is remarkably wide and the tubera basioccipitalia and associated median eminence of the basi-occipital are likewise immense. All this would enable the animal to make a powerful downward sweep with its upper incisors.

In the 1928 collections are two immense occiputs, one of which (Fig. 3), as shown in the accompanying table of measurements (Table I), measures 34 cm. across the occipital condyles as compared with 31.5 cm. in the type skull of *B. grangeri* described by Osborn. This occiput is considerably too wide across the condyles for the atlas described by Cooper, but is apparently about the same size as the occiput figured by Borissiak (Pl. I, fig. 1).

The jaw of *B. grangeri* as restored to fit the skull is slightly larger than the robust jaw No. 26166 (Fig. 4), which is associated with our largest humerus and radius. On the other hand, as noted above, the *B. grangeri* skull is somewhat smaller than our largest occiput (No. 26165). In any case the *B. grangeri* type skull (No. 18650) belongs with the next-to-the-largest animals and is undoubtedly much too large to go with the fore and hind feet (No. 21618) with which it is at present exhibited.

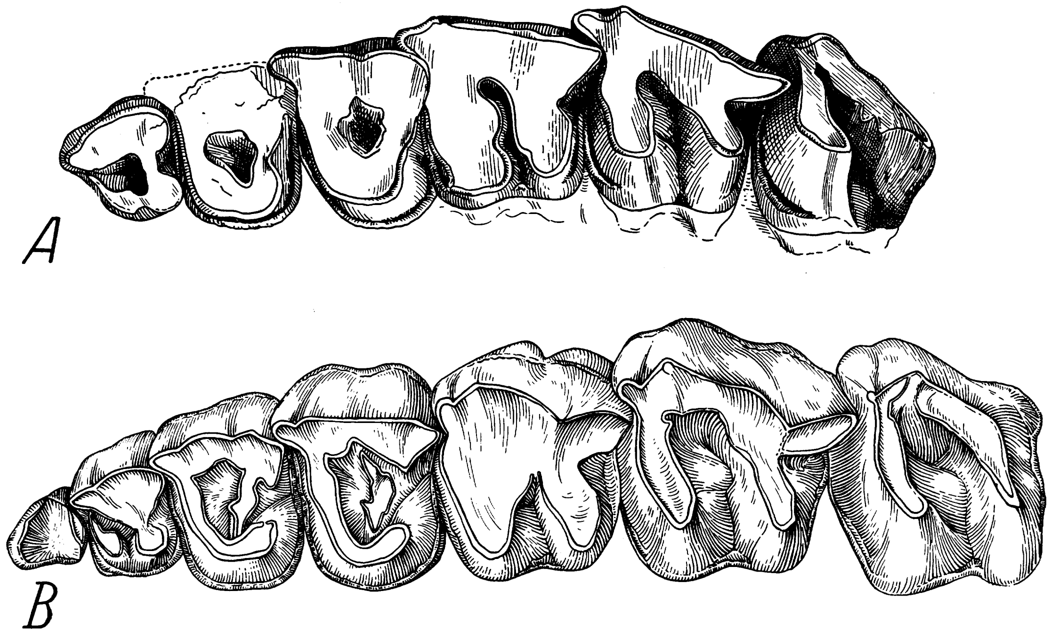


Fig. 2 *A*, *B*. Comparative figures of upper cheek teeth. $\times {}^1/_3$ natural size.

A. "*Paraceratherium bugtiense.*" After Forster Cooper.
B. *Baluchitherium grangeri.* From type skull. P^1, p^2, p^3, restored from right side.

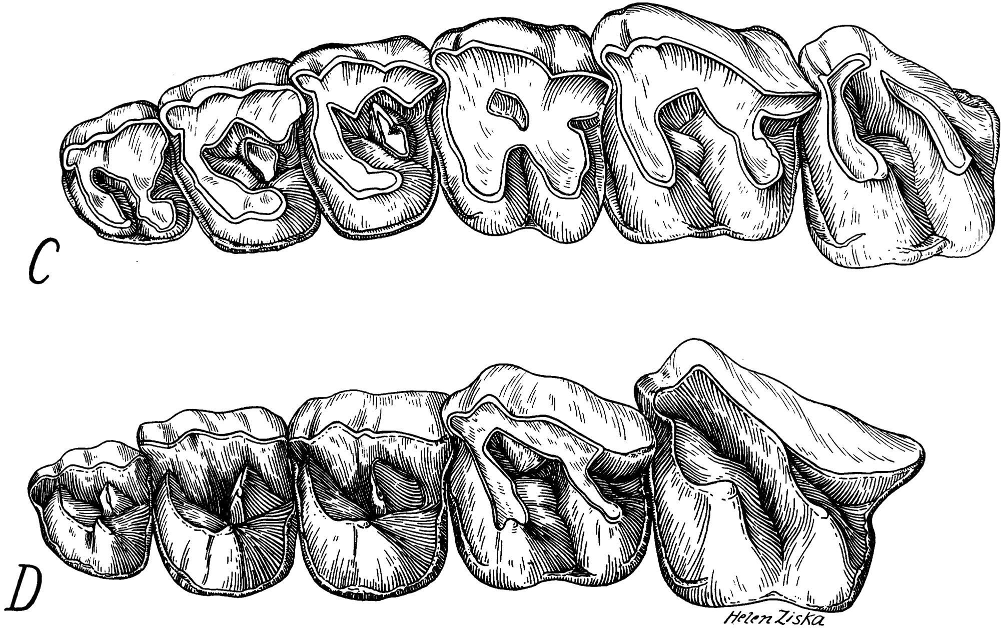


Fig. 2 *C*, *D*. Comparative figures of upper cheek teeth (continued). × 1/3 natural size.
C. *Indricotherium asiaticum*. From cast of older individual.
D. *Indricotherium asiaticum*. From cast of younger individual.
The metalophs of p^3, p^4 are directed backward in *Indricotherium*, somewhat forward in *Baluchitherium*.

TABLE I.—COMPARATIVE SKULL MEASUREMENTS (IN CENTIMETERS)

	No. 18650 *B. grangeri* (type)	No. 26165 (very large)	No. 26167	Boriss. Tab. I
Pmx to condyle........	128.6 (H.F.O.)			
Maximum width across occipital condyle......	31.5	34	29.5	34.1
Width across paroccipital processes.........	33.6	35	36.5	
Height of occiput.......	33	35.5	38	
p^1–m^3................	40.3			
Width across zygomata...	61.4			
Length, condyle to middle of glenoid........	35.5	34	34	(32 est.)

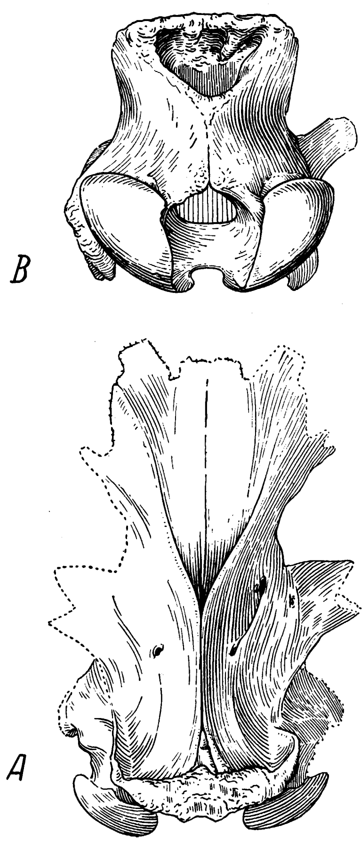


Fig. 3. Posterior part of skull of *Baluchitherium grangeri*. Amer. Mus. No. 26165. × 1/10 natural size.

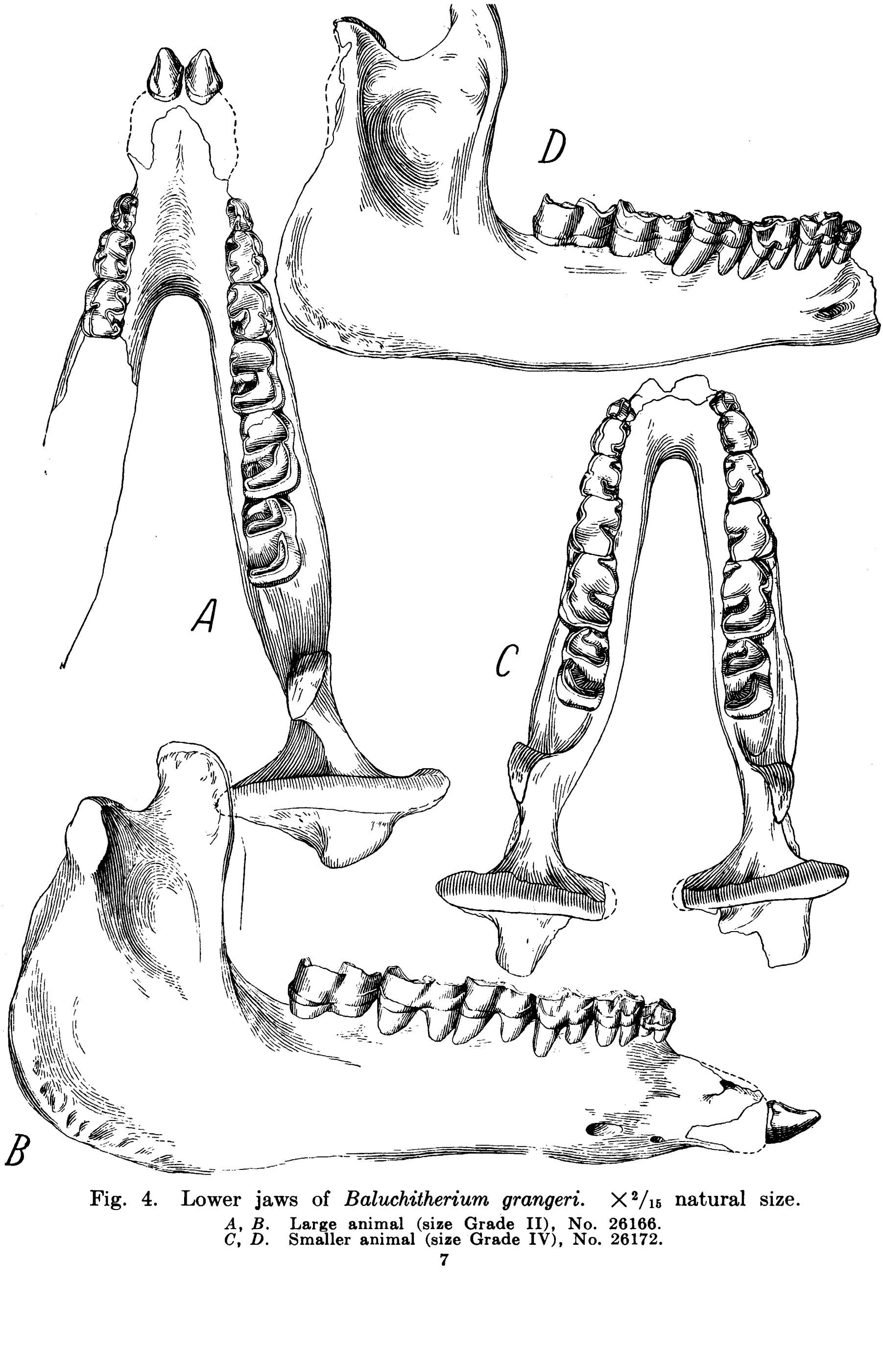


Fig. 4. Lower jaws of *Baluchitherium grangeri*. $\times {}^{2}/_{15}$ natural size.

A, B. Large animal (size Grade II), No. 26166.
C, D. Smaller animal (size Grade IV), No. 26172.

The foramina of the skull (Fig. 5) conform in general with the modern rhinoceros type but are more primitive in the separation of the alisphenoid canal from the foramen ovale. This is conformable with the shallowness and length of the skull. Similarly the pterygoid wings of the alisphenoid, together with the true pterygoid bones, are not deeply extended vertically as they are in modern rhinoceroses. These characters are also related with the relatively slight vertical extent of the cheek teeth.

BRAINCAST.—An incomplete endocranial cast (Pls. I, II) was obtained from the type skull of *Baluchitherium grangeri*. It is more primitive than the brain of *Rhinoceros indicus* as figured by Owen (1852, Pl. XIX) and, as might be expected in so large an animal, the length from the frontal pole to the back of the cerebellum, measuring 125 cm., is only 8 per cent of the skull length, whereas the length of the brain of *Rhinoceros sumatrensis* as figured by Marsh (1884, p. 66) is 17.7 per cent of the skull length.

VERTEBRAE

Our collections include among others the following notable vertebrae: No. 26387 (874), sacrals, lumbars and several dorsals, associated with limb bones of moderate size; No. 26168, two enormous mid-cervicals of doubtful association, the largest vertebrae known in any land mammal; No. 26390 (914), a well-preserved axis, much too small to fit Cooper's atlas; No. 26392 (877), a seventh cervical of intermediate size; No. 26173 (731), a large first dorsal; No. 26169, a fourth (?) dorsal associated with femur, tibia, metatarsus. Close comparisons with Borissiak's plates, which figure the more or less incomplete remains of numerous vertebrae, together with the casts of the atlas and two neck vertebrae received from Professor Forster Cooper, supply data for a fairly satisfactory knowledge of the chief morphological features of the various regions of the vertebral column. As explained below (p. 65), since the bones preserved belong to adults of widely varying sizes, we have endeavored to determine in the case of each bone what its size grade is, and for convenience we have recognized only four grades, hereafter designated as size Grade I, II, III, IV, in descending order.

The ATLAS (Fig. 6), as described and figured by Forster Cooper, is relatively longer and narrower than that of modern rhinoceroses. Its mid-length between the transverse planes of the anterior and posterior articular facets is 26.5 centimeters; its maximum width across the transverse process, 48.3 cm., is 1.81 times its mid-length, whereas in *Rhi-*

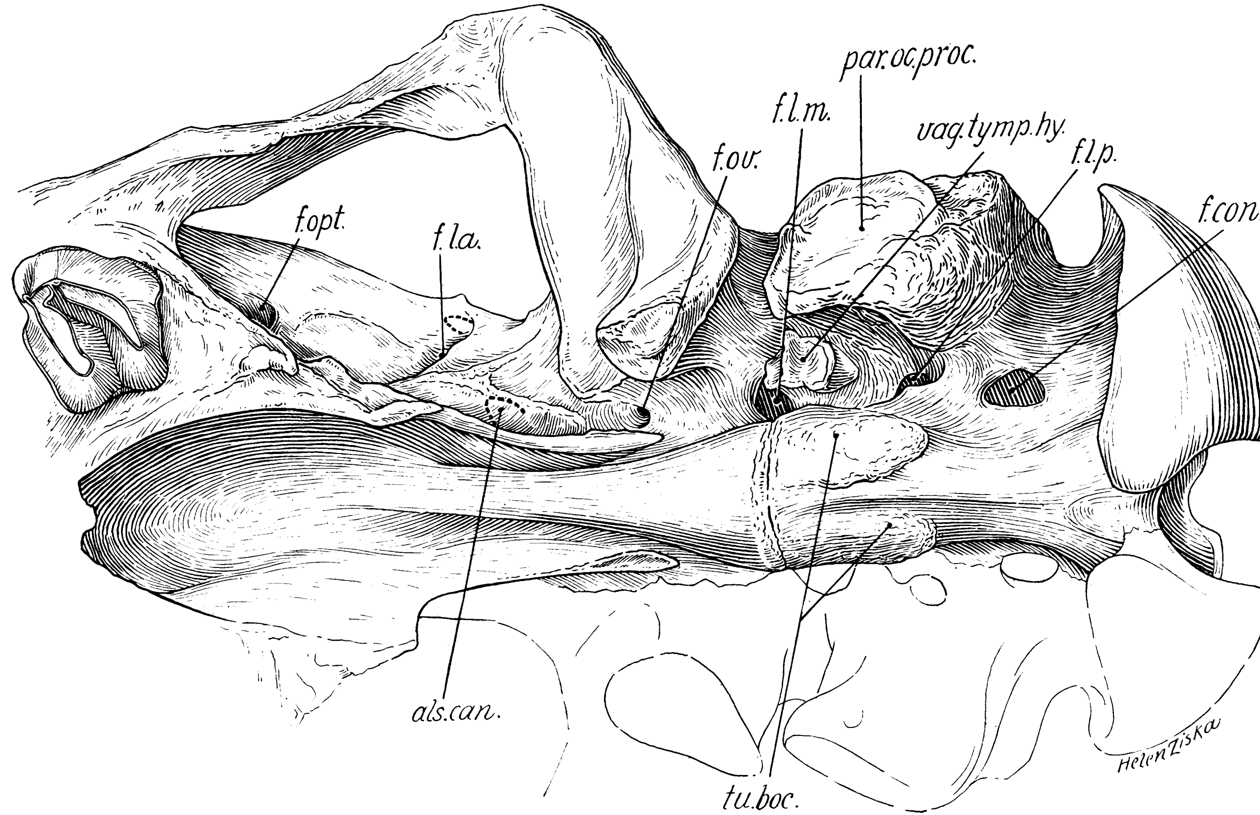


Fig. 5. Basicranial region of *Baluchitherium grangeri*. Type skull. Oblique view of left side.

f.opt. = optic foramen.
f.l.a. = foramen lacerum anterius.
als.can. = alisphenoid canal.
tu.boc. = tubera basioccipitalia.
f.l.m. = foramen lacerum medius.
vag.tymp.hy. = vagina processus tympanicus hyoidei.
par. oc. proc. = paroccipital process.
f.l.p. = foramen lacerum posterius.
f.con. = foramen condylare.

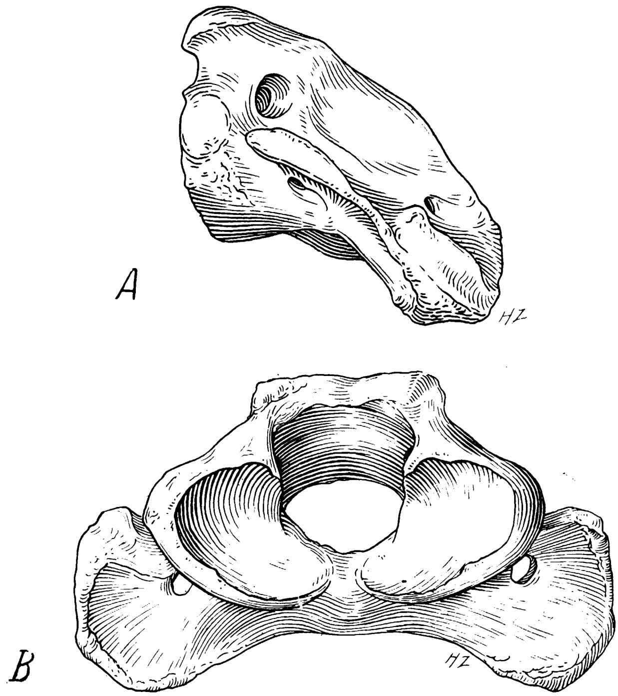


Fig. 6 *A*, *B*. Atlas of *Baluchitherium osborni*. Size Grade II. $\times {}^{2}/_{15}$ natural size.
A. Left side.
B. Front surface. From cast.

noceros sumatrensis the corresponding index is 2.86. The total width across the anterior cotyli (27.7) is, however, too small to receive the gigantic occipital condyles of our largest skull, which measure 34.5 cm. in diameter. If Cooper's atlas were widened to 130 per cent of its present width, its anterior cotyli would be 36 cm. wide and its length increased from 30 to 39 cm. This would be about the right size for the largest occiput. Hence we assign Cooper's atlas to size Grade II.

The anterior articular facets or cotyli are relatively lower and the posterior articular facets of the atlas are spread out more widely than are those of the Sumatran rhinoceros, in accordance with the relatively greater width of the neck. Above the neural tunnel the spine has subsided into a low boss, while its anterior base, tied by ligament to the occiput, finally widens out into a forwardly projecting transverse bar which would greatly limit the dorsal extension of the occiput.

The AXIS (Fig. 7) is represented in our collection by a perfectly preserved specimen, No. 26390 (914), which in spite of its apparently gigantic size, is decidedly too small to fit Cooper's atlas and very small in comparison with our huge mid-cervicals. We therefore regard it as belonging to size Grade III. Its mid-length, from the anterior tip of the neural spine to a transverse plane touching its posterior zygapophysial facets, is 39 cm. as compared with 9 cm. in *Rhinoceros sumatrensis.* Its width across the posterior zygapophysial facets is 22.7 cm., which is 58

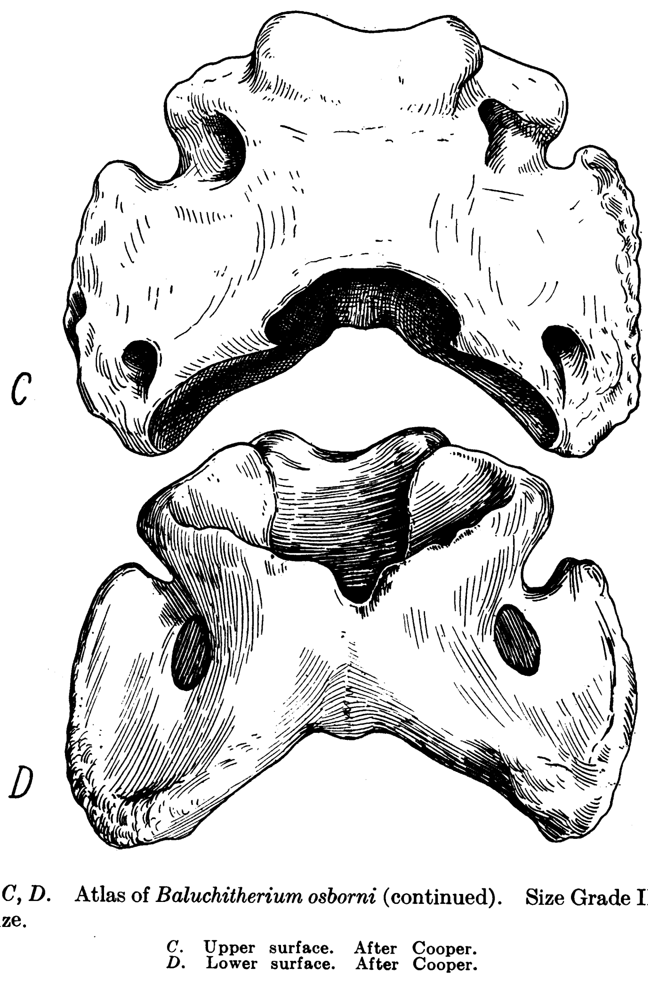


Fig. 6 *C*, *D*. Atlas of *Baluchitherium osborni* (continued). Size Grade II. $\times {}^{2}/_{15}$ natural size.

C. Upper surface. After Cooper.
D. Lower surface. After Cooper.

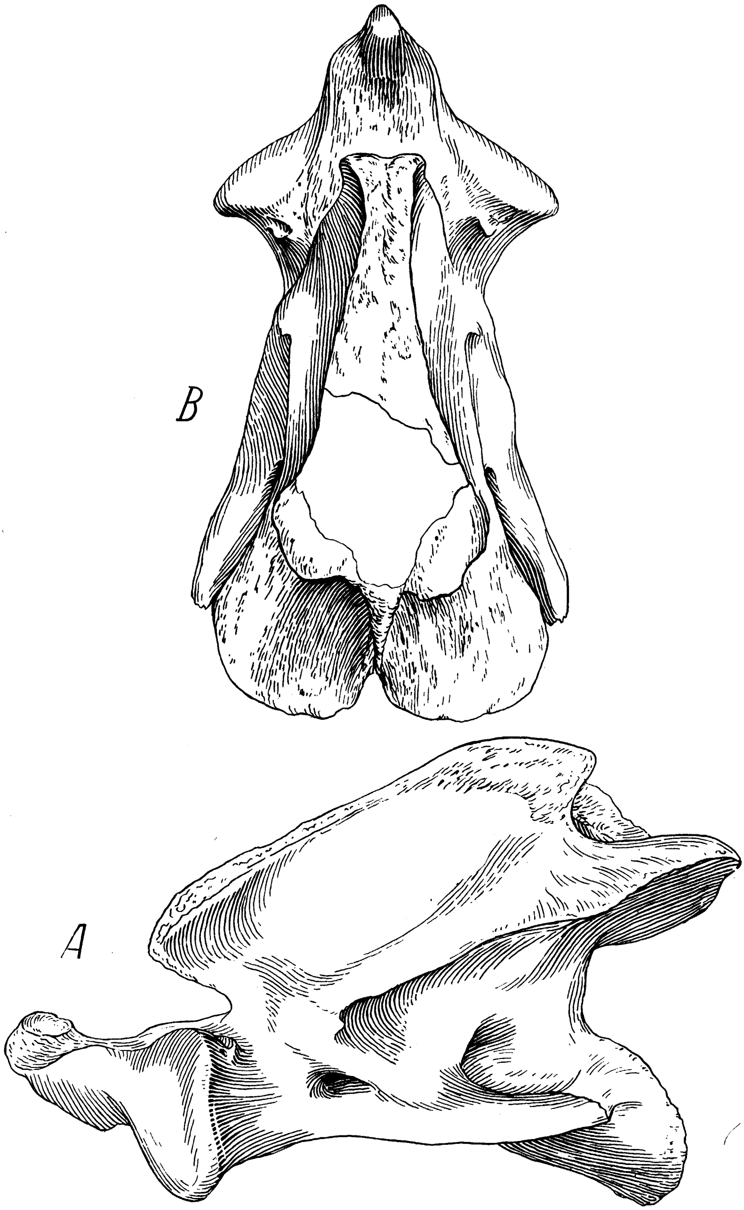


Fig. 7. Axis of *Baluchitherium grangeri*. Size Grade III. $\times {}^{1}/_{5}$ natural size.
A. **Left surface.** ***B.*** **Upper surface.**

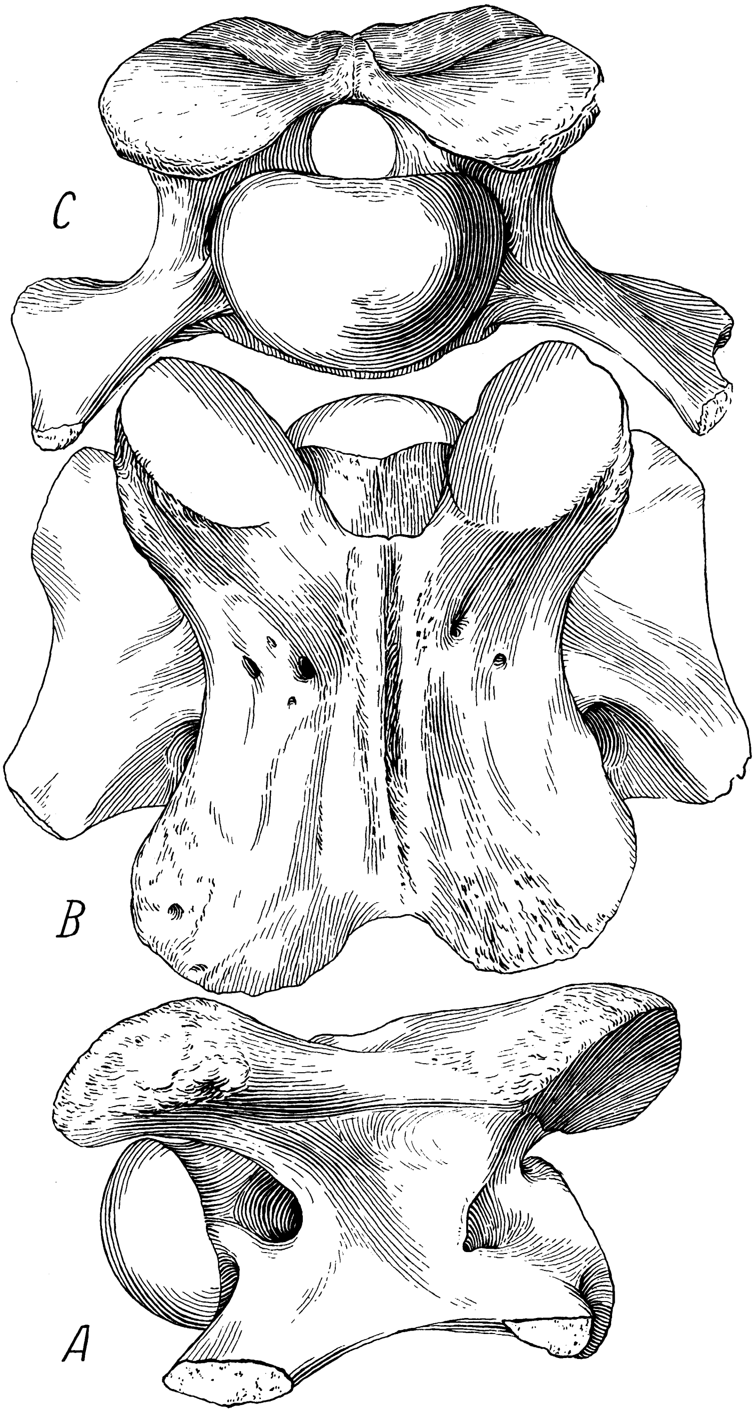


Fig. 8. Fourth cervical vertebra of *Baluchitherium grangeri*. Size Grade I. $\times {}^{1}/_{5}$ natural size.

A. Left lateral view. *B*. Upper surface. *C*. Anterior view.

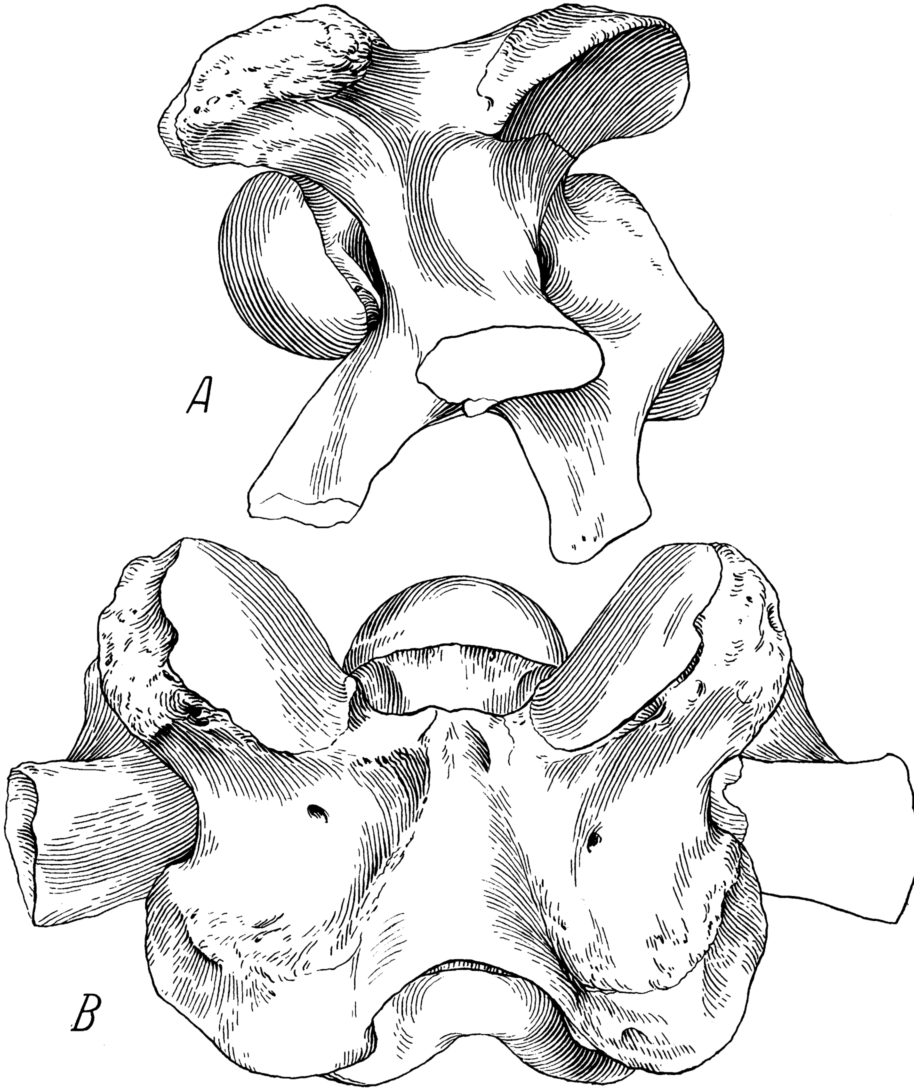
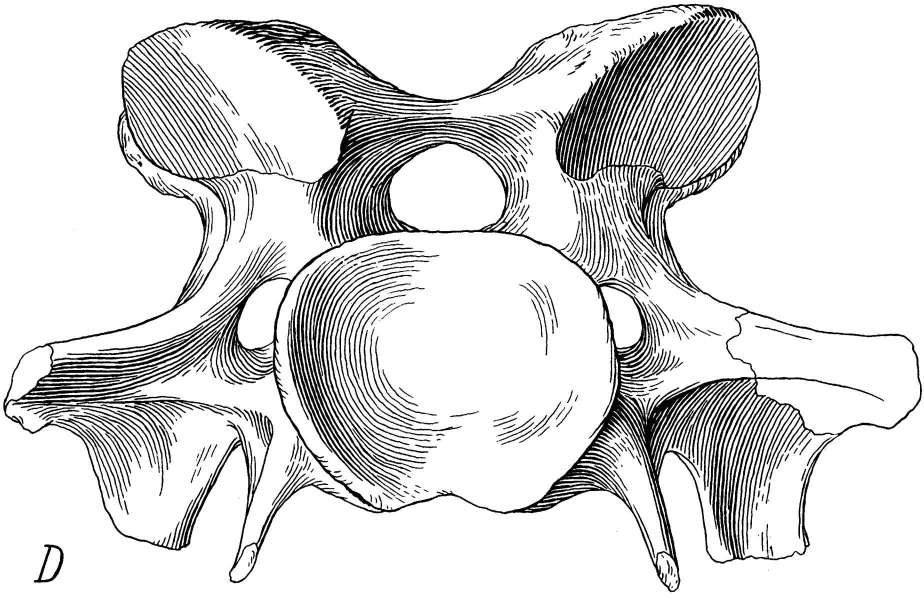
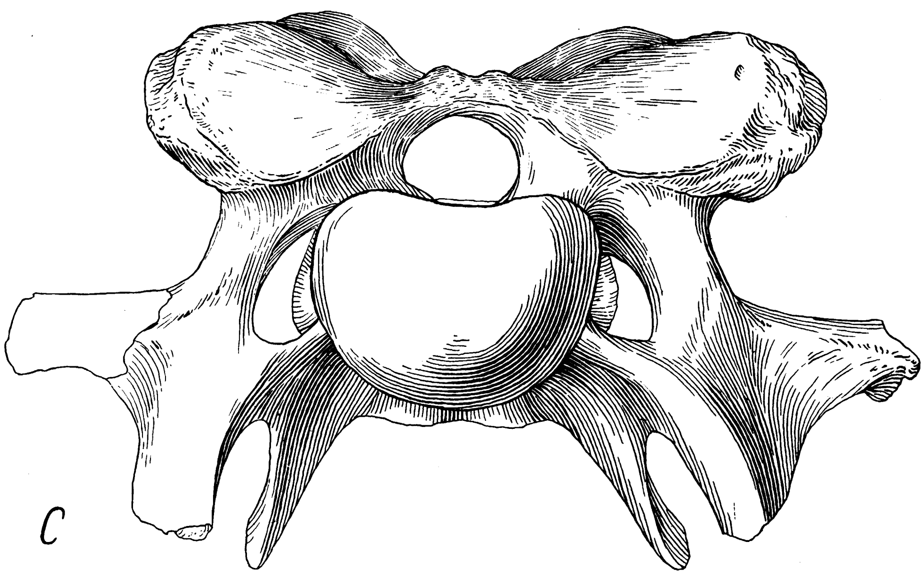


Fig. 9 *A*, *B*. Sixth cervical vertebra of *Baluchitherium grangeri*. Size Grade I. $\times 1/5$ natural size.

A. Left lateral view.
B. Upper surface.



D



C

Fig. 9 *C, D*. Sixth cervical vertebra of *Baluchitherium grangeri* (continued). Size Grade I. × 1/5 natural size.

C. Anterior view.
D. Posterior view.

per cent of its mid-length, whereas in *Rhinoceros sumatrensis* the width is 82 per cent of the length. Its height from the ventral keel to the posterior tip of the neural spine, 30 cm., is but 77 per cent of the mid-length, while in *Rhinoceros sumatrensis* the same measurement is 143 per cent of the mid-length.

The width of the posterior cotylus or cup of the centrum is 18 cm., its height, 12.2 cm., so that it is 1.47 times as broad as it is high, whereas in *Rhinoceros sumatrensis* the width of the cup only equals the height.

As compared with that of *Trigonias osborni*, the width across the posterior zygapophysial facets is relatively less, while the neural spine is long and very low. Thus the axis as a whole is relatively long, low and narrow but presents no feature that appears to be inconsistent with the

TABLE II.—COMPARATIVE CHARACTERS OF THE ATLAS

	Rhinoceros sumatrensis	*Baluchitherium* (Fig. 6)	Draught Horse
Proportions	Very short, very wide	Long, not wide	Very long, narrow
Spine	Prominent	Absent	Very low
Anterior cotyli	Large, high	Very wide, tending to be shallow	Narrow, high, deeply concave
Dorsal anterior border above cotyli		Much thickened, widened, produced forward (tied by ligament to occiput)	Thin, deeply notched
Anterior cotyli, ventral border		Slightly produced anteriorly	Extremely produced ventrally on either side
Transverse process	Very wide, horizontal	Elongate, wide, subhorizontal	Elongate, outer flange sharply decurved
Longitudinal branch of tunnel for occipital artery	Not perforating transverse process	Typically perforating transverse process but variable	Perforating transverse process
Posterior facets	Produced postero-externally; moderate height	Produced postero-externally; shallow dorso-ventrally	Not produced; high
Median posterior ventral process (for insertion of longus colli muscle)	Produced backward beneath body of axis	Present, abbreviate	Truncate, well in front of body of axis

hypothesis that *Baluchitherium* has been derived from a *Trigonias*-like ancestor.

As compared with that of Borissiak's "*Epiaceratherium*," the axis of *Baluchitherium* is almost identical in everything but proportions, being much further evolved in absolute size and relative length (see p. 56 below). Further comparisons are set forth in the accompanying tables.

TABLE III.—COMPARATIVE CHARACTERS OF THE AXIS

	Rhinoceros sumatrensis	*Baluchitherium* (Fig. 7)	Draught Horse
Proportions	Short and high, with high spine	Long, with low spine	Very long and low
Dens epistrophei	Projecting, narrow with oval dorsal facet for floor of neural tunnel	The same	Spout-shaped, with vestige of dorsal oval facet
Anterior articular facets	Convex, oblique	The same	Flattened, transverse
Median ventral notch beneath dens epistrophei	Not developed	The same	Sharp and large
Postarticular cup	Slightly flattened at sides, higher than wide	Much wider than high	Narrow, deeply concave
Mid-ventral posterior keel	Not present	Not present	Prominent
Mid-ventral posterior notch	Prominent	Prominent	Absent
Base of anterior border of neural arch	Notched	The same	Perforated by large foramen
Transverse process	On plane with middle of centrum	The same	Raised above floor of neural tunnel
Post-zygapophyses	Flat	Slightly concave	Concavo-convex
Opposite post-zygapophyses	Widely separated	Strongly approximated	Strongly approximated
Spine, median posterior keel	Pronounced	The same	Abortive

The mid-cervicals are represented in our collection by two vertebrae of colossal size (Figs. 8, 9), which at first sight look more like the vertebrae of sauropod dinosaurs than like those of even the largest land mammals, especially since they bear on each side deep pleurocoeles or rounded cavities which, as Forster Cooper has shown, extend under the floor of

TABLE IV.—COMPARATIVE CHARACTERS OF THE FOURTH CERVICAL VERTEBRA

	Rhinoceros sumatrensis	*Baluchitherium* (Fig. 8)	Draught Horse
General proportions	Very short and high	Long, low and wide	Very long, narrow
Anterior articular facet (ball)	Compressed, much higher than wide, very convex	Wider than high	Higher than wide
Spine	Well developed	Absent	Sessile, flattened
Facets of anterior zygapophyses	Flat, moderately inclined to horizontal	Slightly convex, spreading	Very large, concave, steeper
Facets of posterior zygapophyses	Flat, moderately inclined to horizontal	The same; wide and spreading	Elongated, steeply inclined, less divergent
Lateral processes	Stout, blade-like, with three low lateral processes	Elongate, blade-like, with two processes	Extremely elongate, slender, directed sharply upward posteriorly
Lateral cavities on body of centrum	Not developed	Highly developed	Not developed
Posterior articular facet (cup)	Higher than wide	Wider than high	Subequal
Median posterior ventral keel	Absent	Absent	Pronounced

the neural tunnel and are separated in the midline only by a thin vertical septum. We are inclined to regard these openings not as due to a mysterious adaptation for the lightening of the bones but rather as a growth response to the general principle of fenestration, which in many parts of the vertebrate skeleton results in the strengthening and concentration of bony tissue along the zones of greatest stress and in the opening up of areas where stresses are minimized, as in the temporal fenestrae and pelvic plates of extinct reptiles and mammals.

"Judging from the three known cervical vertebrae," writes Forster Cooper (1923, p. 38) "the length of the neck of *Baluchitherium* was of much the same proportion as that of the horse. The vertebrae are totally unlike those of the Rhinoceros, but show some approximation in general shape and proportions to those of the horse, the only Perissodactyle to which any likeness can be found. There are, however, notable differences which may be explained as adaptations consequent upon the great weight of the skull. The points of resemblances are, however, of

TABLE V.—COMPARATIVE CHARACTERS OF THE SIXTH CERVICAL VERTEBRA

	Rhinoceros sumatrensis	*Baluchitherium* (Fig. 9)	Draught Horse
General proportions	Short	Longer	Very long
Descending flange	Simple	Subdivided into anterior and posterior descending processes	Very elongate
Planes of anterior zygapophysial facets	Facing chiefly inward and upward	Facing more forward	Facing upward and slightly forward
Shape of anterior zygapophysial facets	Rounded, plane	Convex oval	Slightly concave, subcircular, very large
Spine	Fairly large	Absent	Long, low
Inclination of planes of posterior zygapophysial facets	Downward and slightly outward	Slightly downward and outward	Sharply downward and outward
Shape and size of posterior zygapophysial facets	Rounded	Widened	Long ovate, very large
Descending processes	Flange-like, continuous, deep	Divided into long antero - external and postero-internal processes by deep embayment	Skidlike, elongate, shallow; not or barely subdivided
Transverse processes	Directed backward, not widely projecting laterally	Directed outward, projecting widely	Directed outward and backward
Ball of centrum	Higher than wide	Wider than high	Higher than wide
Lateral cavities in body of centrum	Not developed	Highly developed	Not developed
Transverse and vertical diameters of posterior articular facet (cup)	Subequal	Wider than high	Subequal
Concavity of cup	Pronounced	Shallow	Extremely deep
Forward inclination of cup to midline	Moderate	Increased	Extreme
Extension of ball on ventral surface of centrum	Moderate	Slight	Extreme

great interest as examples of convergence in the shape of bones as the result of (presumably) similar stresses and strains in necks of equal proportional length."

After rather prolonged comparative studies of all the material now available we find that, while the atlas and axis to a certain extent suggest the corresponding bones of a horse, the remaining cervical vertebrae present many significant differences, as follows:

(1) In *Baluchitherium* the upwardly facing facets of the anterior zygapophyses are inclined much more forward than in the horse; and both the anterior and posterior zygapophysial facets tend to be small and ovate, whereas in the horse they are very large and subcircular.

(2) Cervicals 4–7 of *Baluchitherium* are all relatively much wider and shorter than in the horse.

(3) The ball-and-cup facets of the centra in *Baluchitherium* are wider than high, the reverse being true in the horse.

(4) The convex facet on the ball of the centrum extends ventroposteriorly beneath the centrum to a much less extent in *Baluchitherium* than in the horse, in which this arrangement permits extreme raising of the neck.

(5) The descending flange in cervical 6 is sharply subdivided into two processes in *Baluchitherium,* while in the horse the subdivision is at most incipient.

(6) The marked relative shortness of the seventh and sixth cervicals in *Baluchitherium* correspondingly limits the upward reach of the neck above the shoulders.

From the facts set forth in our comparative tables we conclude that, contrary to what was shown in previous restorations, the mighty jointed drawbridge which was the neck and skull of *Baluchitherium* was normally directed downward—suspended by the great ligaments and muscles of the neck and occiput and pivoted at the proximal end on the well-buttressed joints of the thorax. The form of the zygapophysial and centrum facets and the relative shortness of the centra indicate wide lateral movements and relatively much shorter reach above the shoulders than in the horse. In brief *Baluchitherium* was essentially a feeder on relatively low bushes.

The principal measurements of the cervicals 4, 6 and 7 are as follows:

	C4	C6 (No. 26168)	C7
Centrum, length between transverse planes touching ball and cup	36. cm.	29.6	18 est.
Centrum, width of ball	19.5	19	18 est.
Centrum, height of ball	12.5	14.6	11 +
Extreme width across transverse process	47.5	58	47
Extreme width across posterior zygapophyses	34	41.5	37
Extreme width across anterior zygapophyses	34	46	44.5
Extreme height, posterior cup to roof of neural arch	23.5	26	23
Length (a.p.), neural arch midline	24.5	17.5	11 est.
Extreme length between transverse planes, anterior and posterior zygapophyses	42.3		

Cervicals 4 and 6 represent our size Grade I, while C 7 is referred to Grade III.

TABLE VI.—COMPARATIVE CHARACTERS OF SEVENTH CERVICAL VERTEBRA

	Rhinoceros sumatrensis	*Baluchitherium* (Fig. 10)	Draught Horse
General proportions	Moderate	Short, broad, low	Long
Transverse processes	Small, not extending below base of centrum	Massive, extending well below base of centrum	Slender, upturned, well above base of centrum
Planes of anterior zygapophysial facets	Inclined slightly upward and inward	Inclined forward and upward	Inclined upward and inward
Shape of anterior zygapophysial facets	Subcircular, plane	Oval, convex	Very large, ovate and plane
Spine	Large and high	Presumably low	Low, delicate
Inclination of posterior zygapophysial facets	Chiefly downward and outward	Downward and backward	Downward and outward
Shape and size of posterior zygapophysial facets	Transverse ovoid	Small and subcircular	Very large, subquadrate
Ball of centrum	Higher than wide	Decidedly wider than high	Higher than wide
Extension of ball on ventral surface of centrum	Moderate	Moderate	Extreme
Transverse diameters across neural arches compared with transverse diameter of posterior articular facet (cup)	Not much greater	Much greater	Subequal

The FIRST DORSAL (Fig. 11) vertebra seems to be of about the right size to fit with the seventh cervical and to belong to an animal of size Grade III. The centrum is 20.5 cm. long and 17.5 wide (ball) and the maximum spread across the lateral processes is 46.5.

As compared with the first dorsal of a large draught horse, the side view of our specimen is moderately short, relatively less elongate; the planes of its anterior zygapophysial facets face upward and forward, whereas in the horse they face upward and inward; the facets themselves are of moderate size, convex oval, while in the horse they are very large

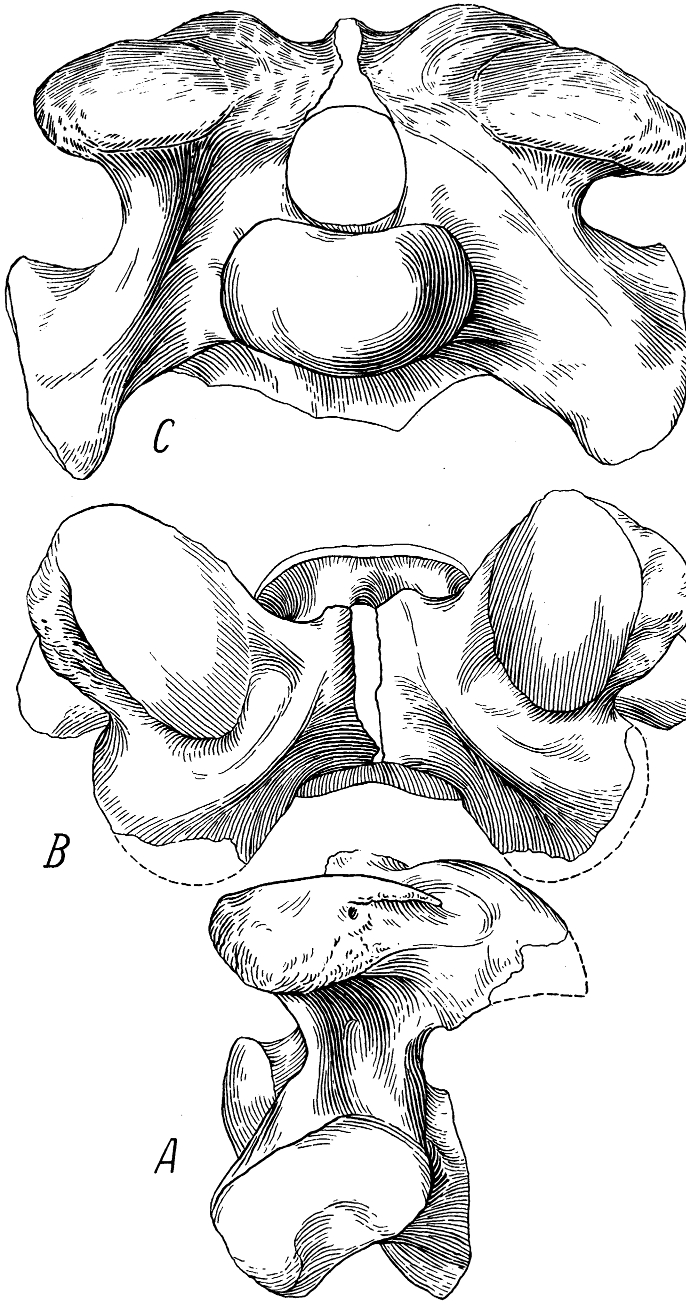


Fig. 10. Seventh cervical vertebra of *Baluchitherium grangeri*. Size Grade III. $\times 1/5$ natural size.

A. Left lateral view. *B*. Upper surface. *C*. Anterior view.

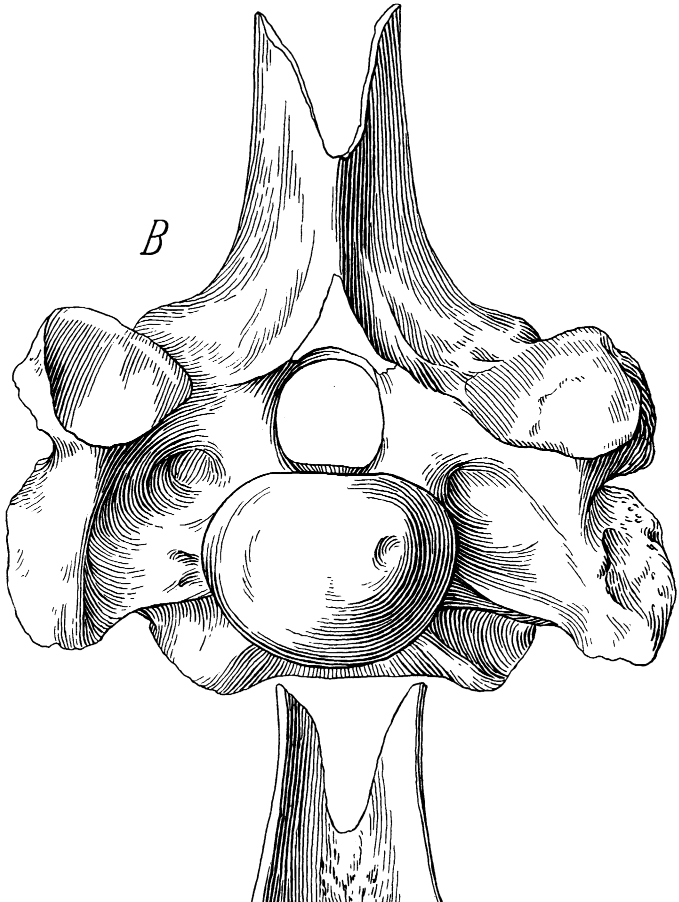


Fig. 11. First dorsal vertebra of *Baluchitherium grangeri*. Size Grade III. $\times 1/5$ natural size.

A. Posterior view. *B*. Anterior view.
(For lateral view see Fig. 12*A*.)

and flat oval. The spine is very long, instead of being short and directed forward as in the horse. The excavation along the back of the spine is extremely developed, whereas in the horse it is absent. The area of the posterior zygapophysial facet as compared with that of the anterior zygapophysial facet is reduced, while in the horse it is greatly reduced. The median keel on the inferior surface of the centrum is absent, in contrast with the well-developed state in the horse. Finally the prolongation of the ball upon the antero-ventral surface of the centrum is moderate, while in the horse it is marked. In all these features except the excavation along the back of the spine the first dorsal of *Baluchitherium* is nearer to that of the recent *Rhinoceros sumatrensis* than to that of the horse.

The SECOND DORSAL (Fig. 12) of a very small animal (not otherwise described as to size) resembles the first dorsal except that it is less extended transversely and has a more backwardly inclined neural spine; the central ball is more circular, the rib facets larger.

The FOURTH DORSAL (Fig. 13) differs from the first especially in the extremely small size of the facets of the anterior zygapophysis, in the pentagonal contour of the anterior articular surface of the ball of the centrum, in the smaller transverse process and in the higher position of the dorsal surface of the transverse process as compared with the body of the centrum. This vertebra differs from that of *Rhinoceros sumatrensis* in the deep vertical excavation of the posterior border of the neural spine and in the consequent wider separation of the posterior zygapophysial facets. From that of the horse it differs in the lesser development of the metapophyses above the transverse process, in the relatively much smaller and lower capitular facets on either side of the concave posterior facet of the centrum. The horse also lacks the deep posterior excavation of the neural spine and has a sharp ventral keel on the centrum.

The FIFTH(?) DORSAL is apparently represented in Borissiak's Tab. IV, figs. 4a, b, c. Here the spine was set farther back than in D 3, the metapophyses were high and prominent and the facets for the capitula were higher up, flanking the top of the posterior facet of the centrum. The chief differences from *Rhinoceros sumatrensis* are the greater size and erect position of the metapophyses. As compared with the same bone of the horse, the anterior and posterior concave facets for the capitula are less prominent and less deeply concave, while the metapophyses are less extended anteroposteriorly.

For the EIGHTH(?) DORSAL also we must rely on Borissiak's plate

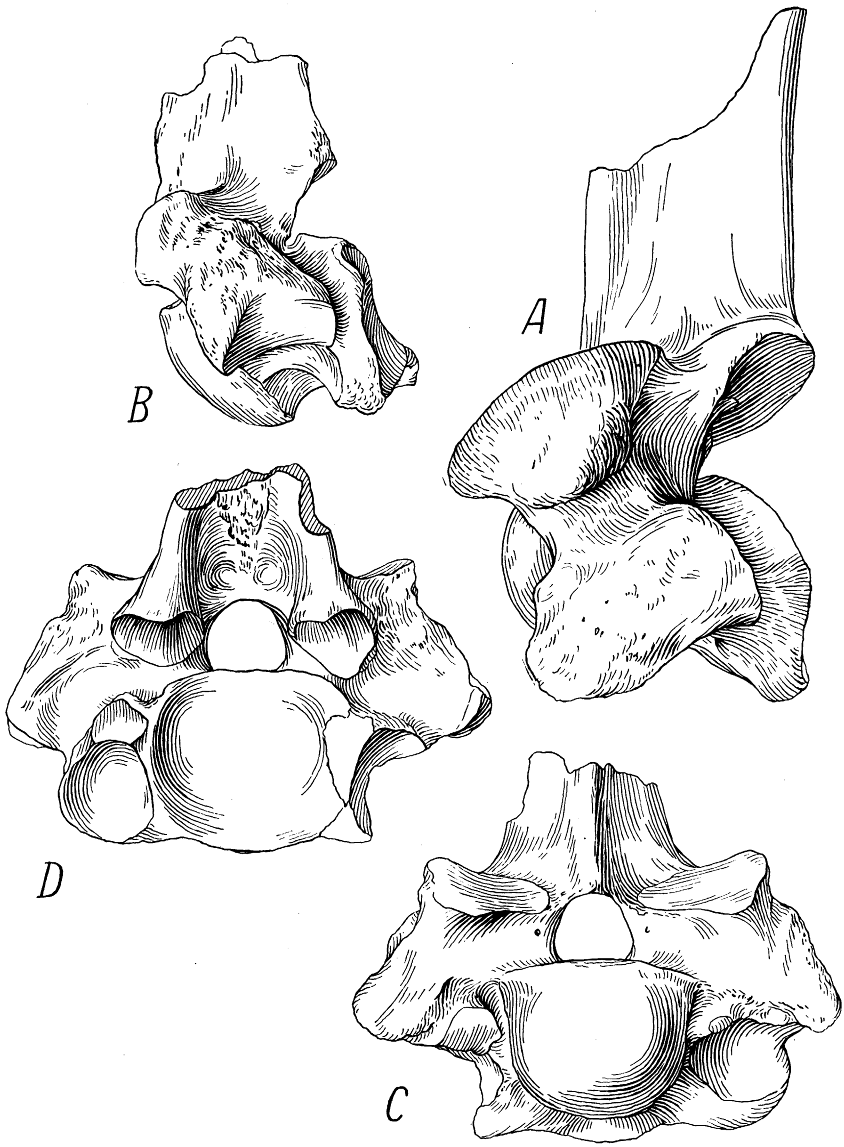


Fig. 12. First and second dorsal vertebrae of *Baluchitherium grangeri*. $\times 1/5$ natural size.

A. Left lateral view of first dorsal, larger animal. Size Grade III. (Cf. Fig. 11.)
B. Left lateral view of second dorsal, very small animal.
C. Anterior view, very small animal.
D. Posterior view, very small animal.

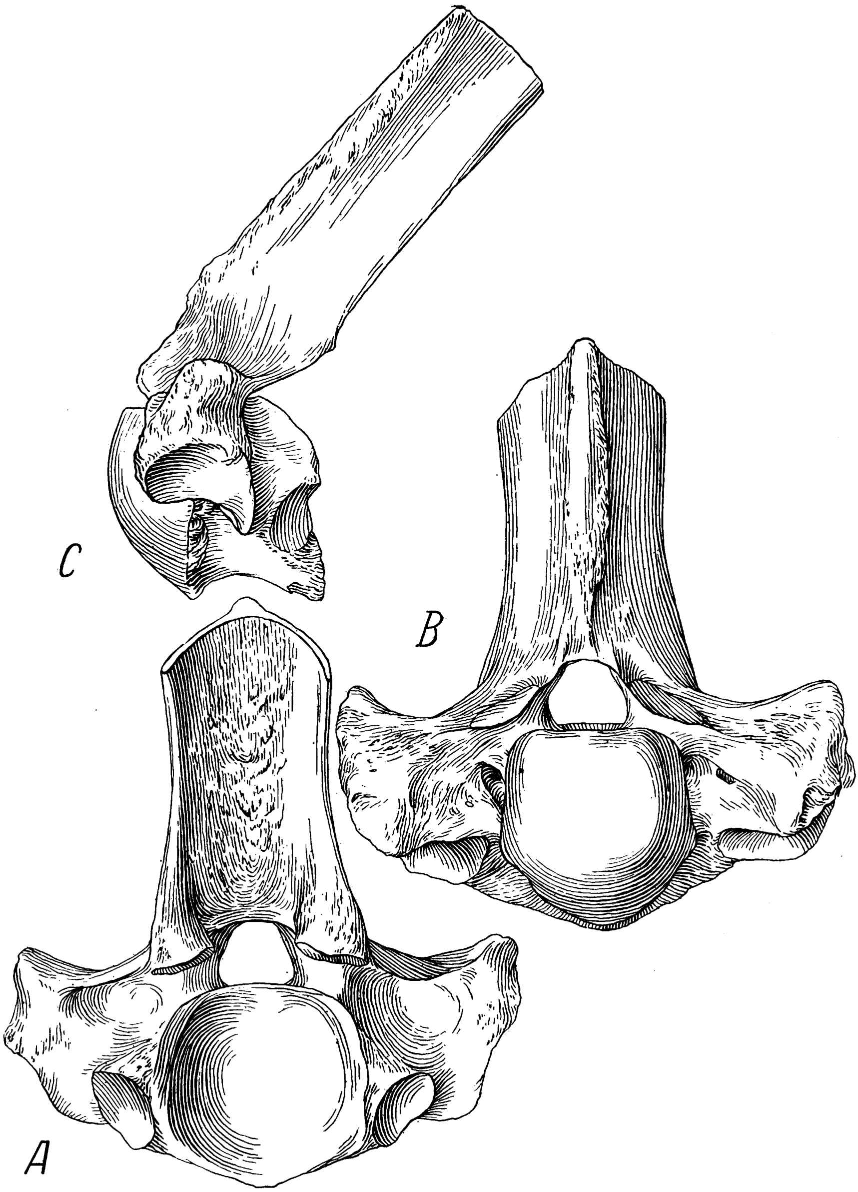


Fig. 13. Fourth dorsal vertebra of *Baluchitherium grangeri*. Size Grade IV. $\times 1/5$ natural size.

A. Posterior view. *B.* Anterior view. *C.* Left lateral view.

(Tab. IV, fig. 5), where a vertebra of this vicinity is shown with a relatively short spine and with the entire transverse process directed outward and upward. The facets of the anterior zygapophyses are nearly horizontal. There is a rather close general correspondence with D 8 of *Rhinoceros sumatrensis*. In the horse the spine is relatively much longer and the rib facets very large and cup-like.

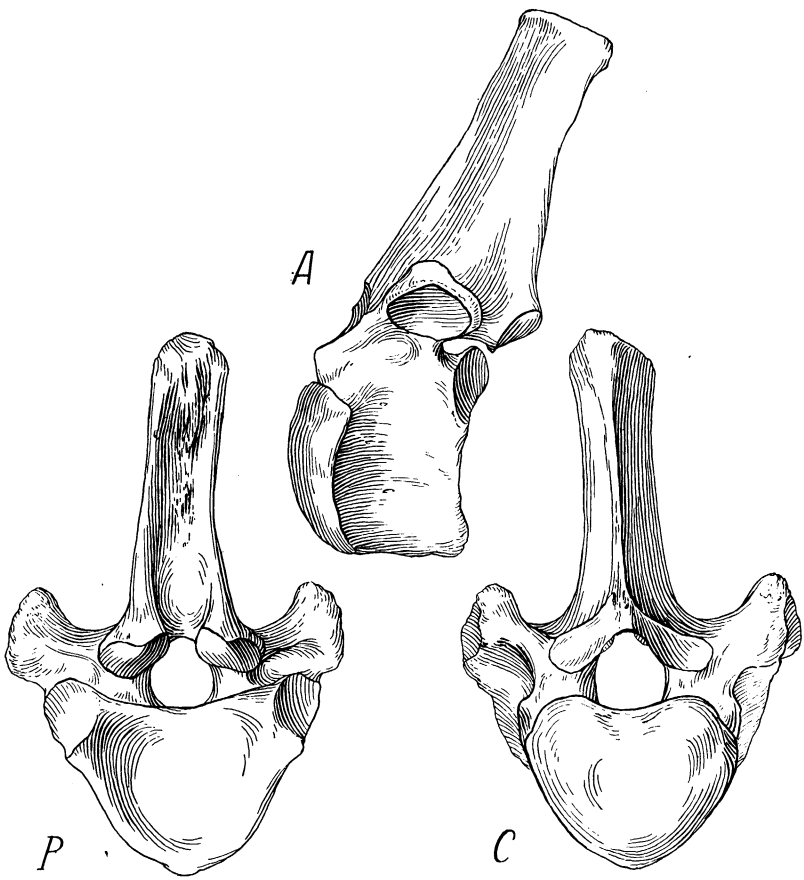


Fig. 14. Twelfth dorsal vertebra of *Baluchitherium grangeri*. Size Grade IV. $\times {}^1/_5$ natural size.

A. Left lateral view. *B*. Posterior view. *C*. Anterior view.

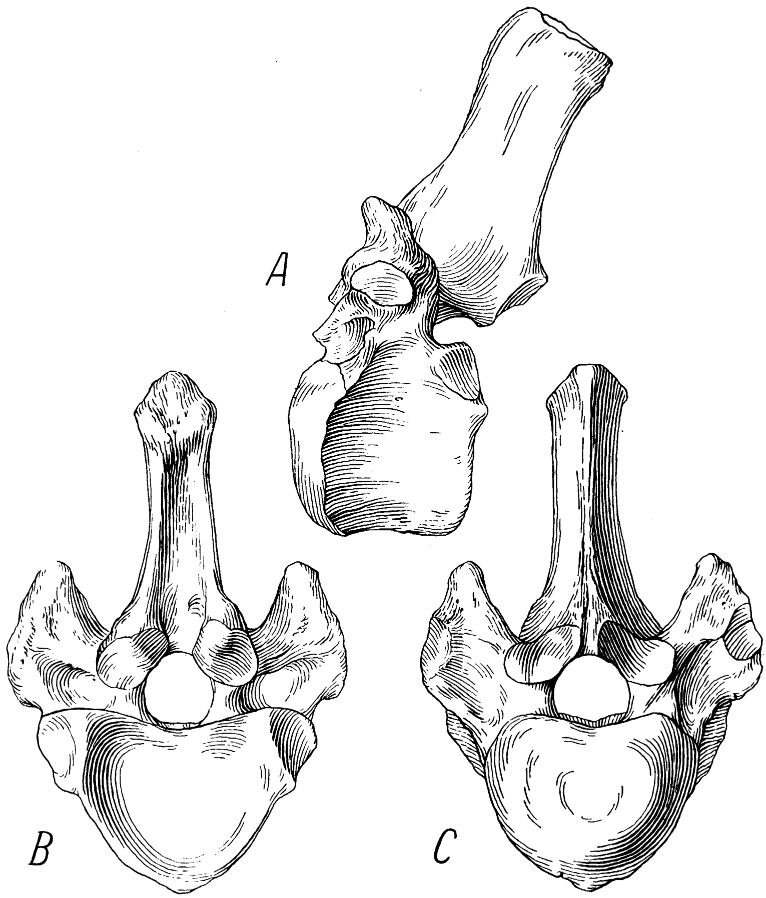


Fig. 15. Thirteenth dorsal vertebra of *Baluchitherium grangeri*. Size Grade IV. × $^1/_5$ natural size.

A. Left lateral view. *B.* Posterior view. *C.* Anterior view.

In the TENTH(?) DORSAL (Borissiak, Tab. IV, fig. 6a, b, c) the large spine is somewhat sigmoid in side view. There is hardly any lateral projection of the transverse processes and the small rib facets lie lateral to the pedicles of the neural arch, although extending down on the uppermost levels of the posterior articular face of the centrum. The latter is deep vertically and narrow transversely. D 10 of *Rhinoceros sumatrensis* has a relatively shorter spine, much wider transverse processes, higher metapophyses. In the horse, D 10 has much larger facets for the capitulum and relatively wider centra.

The TWELFTH and THIRTEENTH DORSALS (Figs. 14, 15) are represented in our collection by two well-preserved vertebrae (No. 26387)

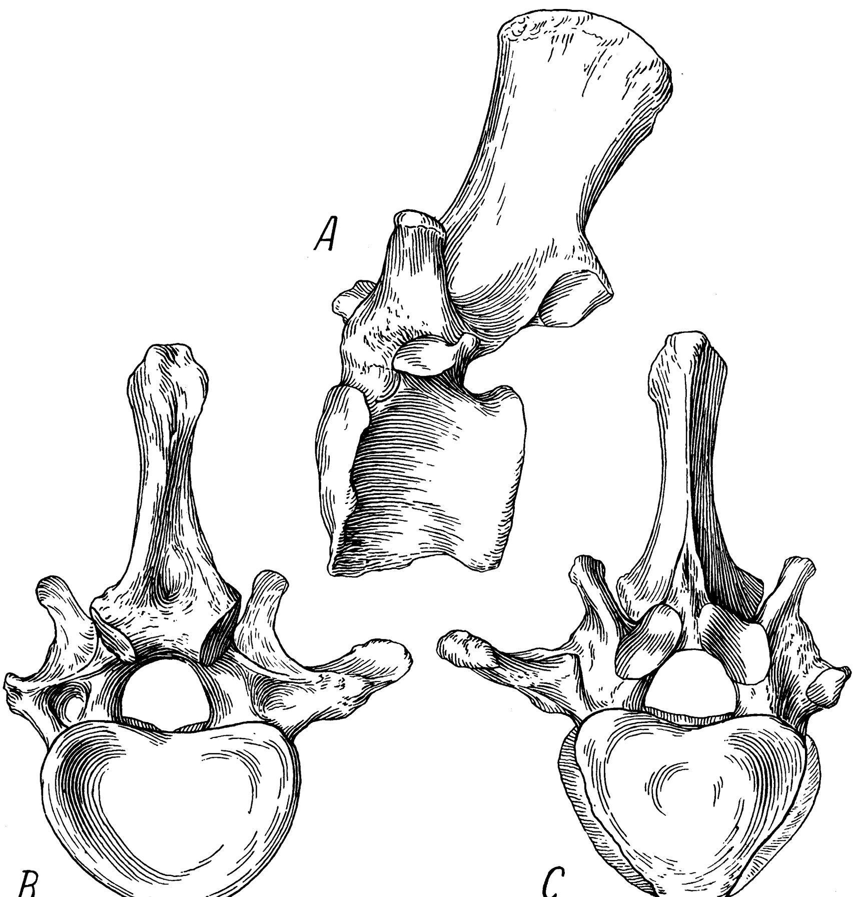


Fig. 16. First lumbar vertebra of *Baluchitherium grangeri*. Size Grade IV. $\times 1/5$ natural size.

A. Left lateral view. *B.* Posterior view. *C.* Anterior view.

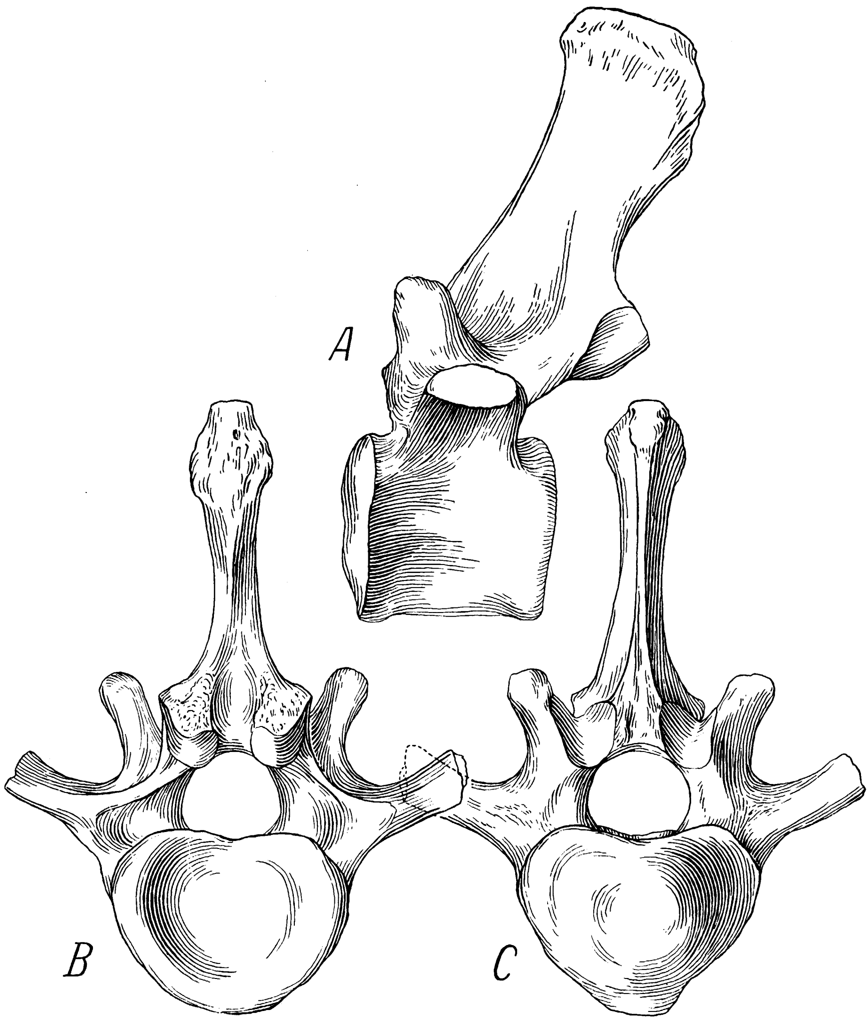


Fig. 17. Second lumbar vertebra of *Baluchitherium grangeri*. Size Grade IV. $\times 1/5$ natural size.

A. Left lateral view. *B*. Posterior view. *C*. Anterior view.

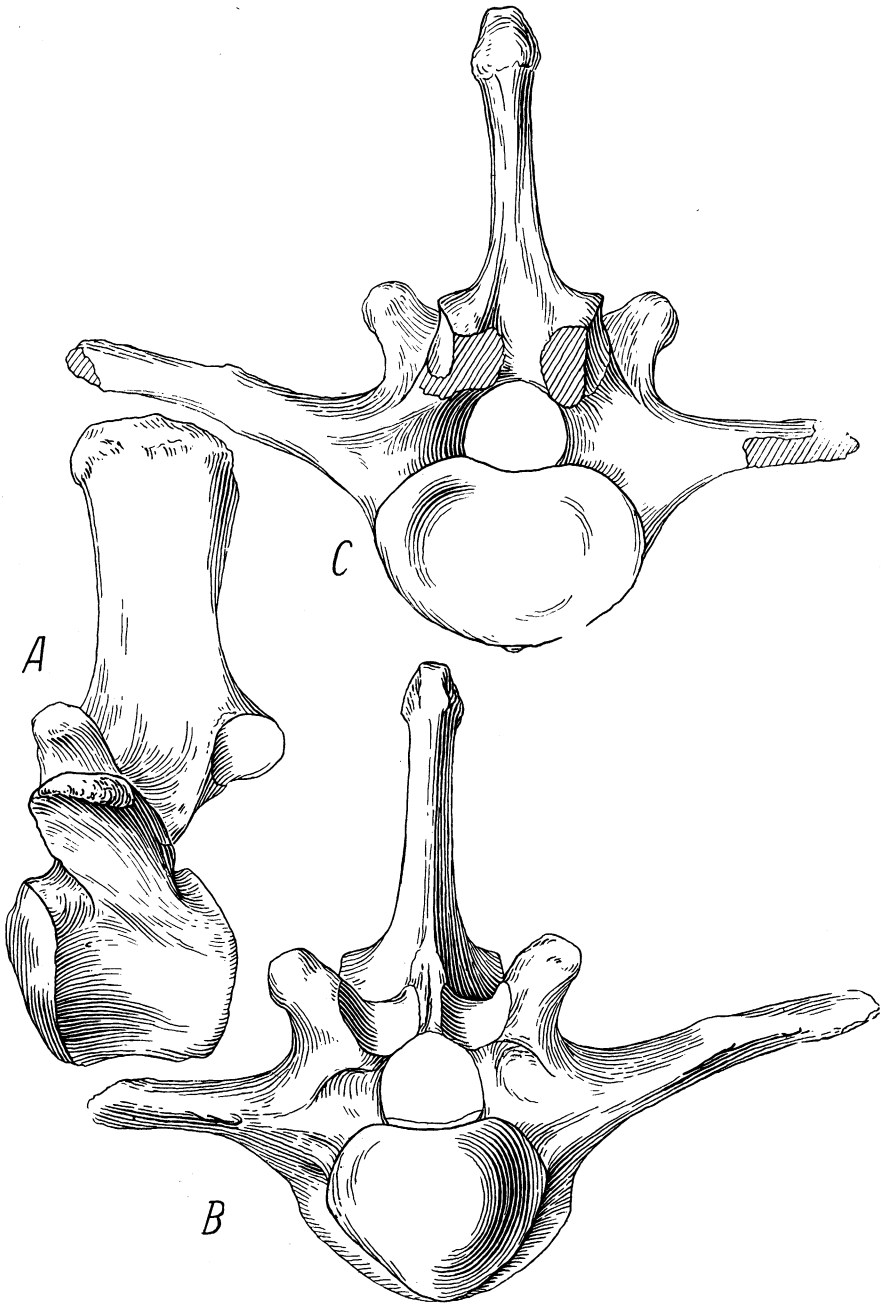


Fig. 18. Third lumbar vertebra of *Baluchitherium grangeri*. Size Grade IV. $\times {}^1/_5$ natural size.

A. Left lateral view. *B.* Anterior view. *C.* Posterior view.

associated with lumbar and sacral vertebrae and limb bones. This animal belongs to our size Grade IV. In the thirteenth dorsal the top of the neural spine is 34 cm. above the level of the base of the centrum; length of the centrum, 13 cm., maximum width of same, 16 cm.

Both D 12 and 13 have much higher spines than the corresponding vertebrae of *Rhinoceros sumatrensis* but are in this respect not so different from the white rhinoceros. The metapophyses, however, are more conspicuous. The postzygapophysial facets are beginning to be subdivided by a median eminence into inner and outer planes corresponding to concave facets on the anterior zygapophyses, whereas in both *Rhinoceros sumatrensis* and *Ceratotherium simum* they are flat. The neural spines retain shallow posterior excavations throughout their length as in *Ceratotherium simum,* whereas in *Rhinoceros sumatrensis* the very short spines are keeled posteriorly.

The lumbars, first, second and third, are well-preserved bones (Figs. 16, 17, 18) of the same series of relatively small-sized animals. The principal measurements of these lumbars are as follows:

	L1	L2	L3
Height to top of spine	37 cm.	41 cm.	42 cm.
Length, centrum (side)	13	14.5	14.5
Max. width, centrum (post.)	16.5	15.5	17.5

The lumbars are characterized by their long, large spines, erect metapophyses, keeled centra and small anterior zygapophysial facets on L1, L2, and deeply concave facets on L3. In *Rhinoceros sumatrensis* the spines are short and antero-posteriorly longer, the metapophyses vestigial and the zygapophysial facets relatively larger. These conditions are accentuated in *Ceratotherium simum.*

The transverse processes of the first lumbar, although short and truncate distally, are true ribs, articulating by a vestigial capitulum with the antero-superior corner of the centrum and by a much widened tuberculum with an oval facet on the lateral process. In our *Rhinoceros sumatrensis* the first lumbar rib is detached on the right side, leaving a large articular surface on the transverse process. Traces of this separateness of the rib are visible on L1 of a large white rhinoceros but not on our draught horse.

In the second and third lumbars the long upwardly arched transverse processes show no trace of having arisen as ribs. The fourth lumbar is missing. The fifth (?), as represented in Borissiak's Tab. V, Figs. 5a, b, c, has a large low transverse process and widely oval anterior and posterior articular facets of the centrum. The spine is fairly high, the metapophyses prominent and forwardly directed. There is a large oval facet for the sacral rib on the back of the transverse process.

In *Trigonias* the last lumbar vertebra was free from the sacrum but in *Rhinoceros sumatrensis* it has become enlarged and integrated with the sacrum, forming indeed the largest and widest member of the sacral series. The same seems to have been true in *Baluchitherium.*

The SACRUM (Fig. 19) is incompletely preserved in the same series (No. 26387). Of the five spines preserved the first and highest seems to represent the last lumbar (or lumbo-sacral), which is also represented by the very large flaring transverse process of the left side. The last spine belongs to the first coccygeal or sacro-caudal vertebra. The spines are

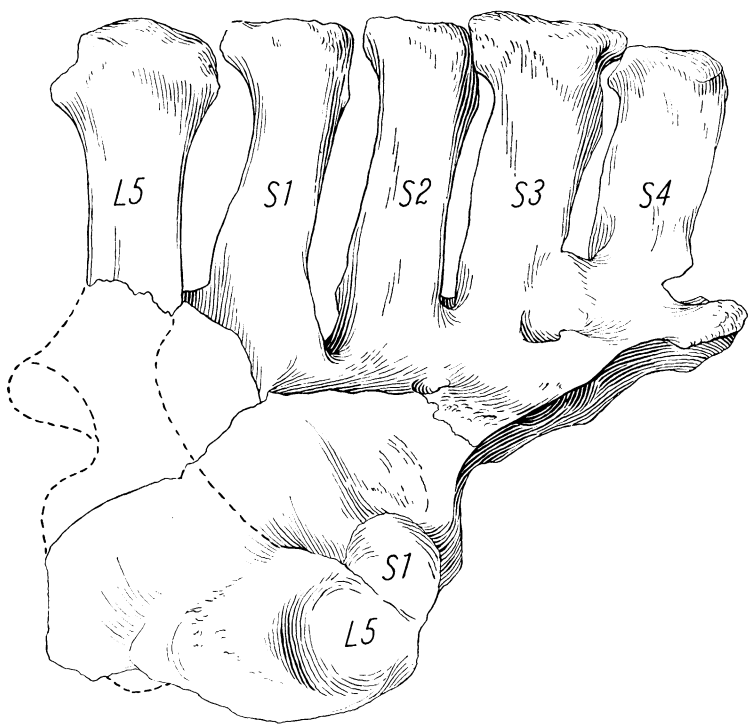


Fig. 19. Fifth lumbar vertebra and sacrum of *Baluchitherium grangeri.* Size Grade IV. $\times 1/5$ natural size.

Left lateral view.

expanded and very rugose on top, not compressed as in *Rhinoceros sumatrensis*. An antero-posterior series of four pairs of large nerve exits on the under side lie between the transverse processes of the three true sacral vertebrae, the centra of which are flat beneath. There is a very large lateral articular surface for the ilium on the transverse process of the great lumbo-sacral, together with a much smaller iliac facet on the transverse process of the first true sacral and the minute iliac facets of the second and third sacrals. The lumbar and sacral regions of *Baluchitherium* are widely different from those of a horse. In the draught horse there are six lumbars, of which the last three have the flattened form of lumbo-sacrals. Possibly the sixth represents an appropriated first sacral.

The CAUDAL VERTEBRAE are not preserved but to judge from the relatively large size of the sacro-coccygeal vertebrae, the tail was not materially different except in absolute size from that of *Trigonias*.

To sum up, the cervical vertebrae of *Baluchitherium*, in spite of their specializations for huge size, including greater relative width, loss of spines, development of pleurocoeles, downward and forward turning of anterior zygapophysial facets, etc., exhibit no peculiarities which are not apparently derivable from the far more primitive condition preserved in *Trigonias* and *Allacerops* ("*Epiaceratherium*") *turgaicum*. Thus to derive the atlas of *Baluchitherium* from that of *Trigonias* one would have to increase the length of the transverse processes faster than their width. At the same time the transverse diameters of the cotyli for the occipital condyles would have to be accelerated. The axis of *Baluchitherium* has evidently been derived from a form like that of *Allacerops* ("*Epiaceratherium*") merely by a differential lengthening of the bone as a whole.

The fourth cervical of *Baluchitherium* is relatively longer, lower and much wider than that of *Trigonias*, the ball of the centrum is widened and the cup still more so; the spine, well developed in the primitive *Trigonias*, has disappeared and the anterior zygapophysial facets have been turned more forward. The transverse blade is more horizontal in position and tends to be subdivided into anterior and posterior divisions. Deep lateral cavities have developed on the centrum.

The sixth cervical of *Baluchitherium* is relatively longer and wider than that of *Trigonias* and has lost its spine; its downwardly directed flange is sharply subdivided into anterior and posterior wings, its centrum is deeply excavated and the anterior zygapophysial facets face more forward, the posterior ones more backward, this favoring lateral rather than vertical movements. The seventh cervical as compared with that of *Trigonias* is short, broad and low, with low spine; its very massive transverse process extends well below the base of the centrum. The centrum is extremely wide and the ball is somewhat more produced

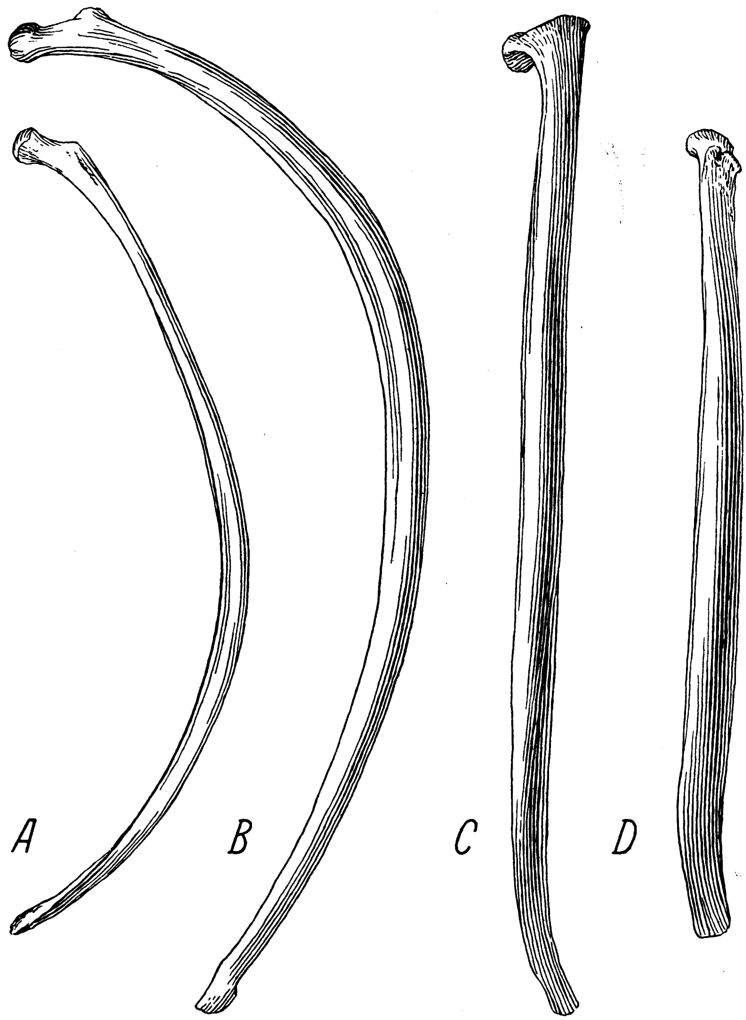


Fig. 20. Ribs of *Baluchitherium grangeri*. (Small animal, size Grade IV, No. 26387.) $\times {}^1/_{10}$ natural size.

A. Sixth dorsal rib, left. Anterior view.
B. Eighth dorsal rib, left. Anterior view.
C. Eighth dorsal rib, left. Lateral view.
D. Tenth dorsal rib, left. Lateral view.

on the ventral surface than in *Trigonias*. The planes of the postzygapophysial facets are directed more downward and backward and not so much outward. The pedicles or pillars of the neural arches are massive and greatly widened.

Thus the neck of *Baluchitherium* was capable of freer lateral movements than that in the *Trigonias*-like ancestor.

The dorsal, lumbar and sacral vertebrae of *Baluchitherium* are like-

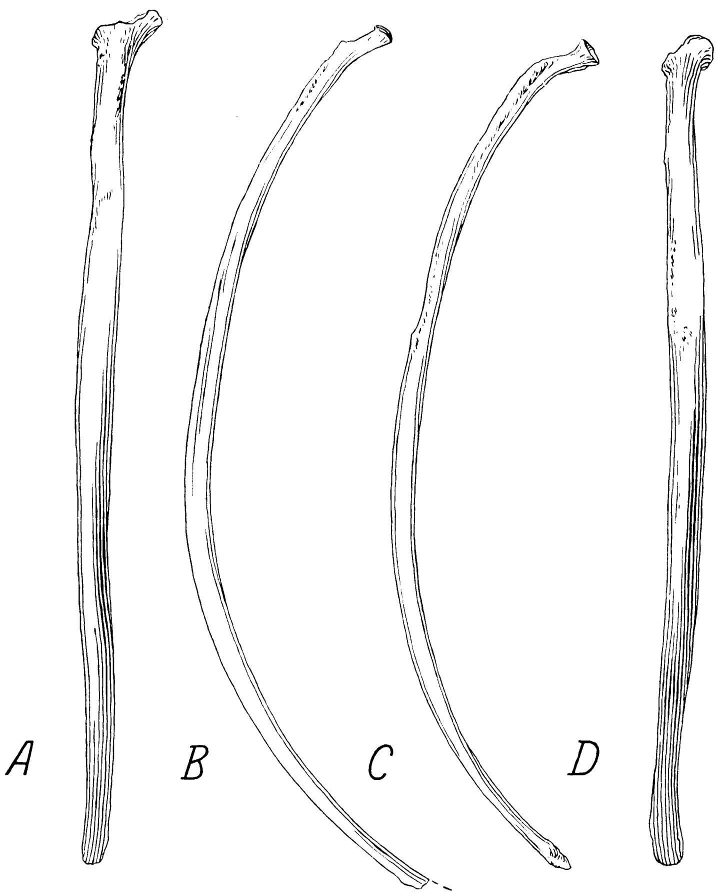


Fig. 21. Ribs of *Baluchitherium grangeri* (continued). (Small animal, size Grade IV, No. 26169.) $\times$ 1/10 natural size.

A. Tenth dorsal rib, right. Lateral view.
B. Tenth dorsal rib, right. Anterior view.
C. Twelfth dorsal rib, right. Anterior view.
D. Twelfth dorsal rib, right. Lateral view.

wise all readily derivable from the corresponding parts of primitive subcursorial rhinoceroses and differ very widely from those of the horse. Among their more conspicuous features are the posterior excavations of the long neural spines of D1–D4, the emphasis of the erect metapophyses, which are depressed or relatively feeble in recent rhinoceroses and the

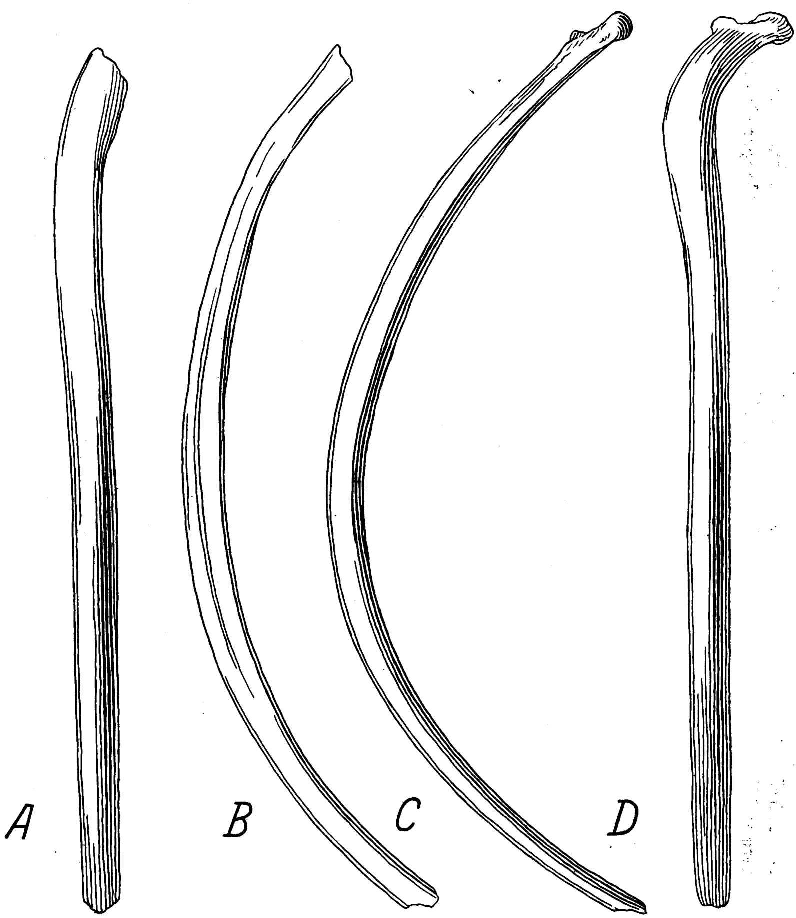


Fig. 22. Ribs of *Baluchitherium grangeri* (continued). (Large animal, size Grade II, No. 26166.) $\times 1/10$ natural size.

A. Thirteenth (?) dorsal rib, right. Lateral view.
B. Thirteenth (?) dorsal rib, right. Anterior view.
C. Fourteenth dorsal rib, right. Anterior view.
D. Fourteenth dorsal rib, right. Lateral view.

TABLE VII.—COMPARATIVE MEASUREMENTS OF LIMB BONES WITH PROVISIONAL ESTIMATES (e) BASED PRIMARILY ON ASSOCIATED PARTS

	No. 26387 Grade IV	No. 21618 Grade IV	No. 26169 Grade IV	No. 26166 Grade II	No. 26175 Grade I	*Baluchitherium osborni* Cooper Grade IV	*Indricotherium asiaticum* Bor. Grade II, III, IV
Scapula	80 cm.			(84.5 e)	112 e		
$\frac{S}{H}$	86%						
$\frac{S}{R}$	70%						
Humerus	(90 e)			98.5	120 e	84.0	93.0 Grade III 90.4
$\frac{H}{R}$	(80% e)						
$\frac{H}{F}$	(70% e)						
Radius	112			120	150 e		
$\frac{R}{H}$	(123% e)			124% e			
$\frac{R}{U}$	(86% e)			(90% e)			
Ulna	(130 e)			(135 e)	162 e		120. Grade IV 113 e
$\frac{U}{H}$	(144%)?						
$\frac{U}{R}$	116% e			110%			
Mtc. III	(43 e)	42		53.5	63.5 e	44.	51.5, 54.5, ?60 (Grades II, ?I)
$\frac{\text{Mtc. III}}{H}$				54.5%			
$\frac{\text{Mtc. III}}{R}$				44.5%			

Pelvis (tip ilium to end ischium)	112 (?)				150 e		100 (?) Grade IV)
$\frac{Plv.}{F}$	87% (?)						
$\frac{Plv.}{R}$	100%						
Femur	128.5		119	(139 e)	166 e	120.	123. Grade IV
$\frac{F}{T}$	153%						
$\frac{F}{R}$	114%						
$\frac{F}{Mts. III}$	320%						
Fibula	76+						
Calcaneum	28	26.5					
Tibia	84		80	(92 e)	110 e	79.0	86 Grade III
$\frac{T}{F}$	66% e		67%				
$\frac{T}{R}$	75%						
Mts. III	40.5	39	41		60 e		52, 51 Grade II
$\frac{Mts. III}{F}$	31%		34%				
$\frac{Mts. III}{R}$	35%						
Manus (prox. carpal to ground)	(70 e)	65			107 e		93 e Grade II
$\frac{Manus height}{R}$	62% e						

TABLE VII.—*Continued*

	No. 26387 Grade IV	No. 21618 Grade IV	No. 26169 Grade IV	No. 26166 Grade II	No. 26175 Grade I	*Baluchitherium osborni* Cooper, Grade IV	*Indricotherium asiaticum* Bor. Grades II, III, IV
Pes (top astragalus to ground)		60		77 e	92 e		95 e Grade I
Pes / Manus		90%					
Length between center manus and pes	294 e	241		(321 e)			
Length / Mtc. III		600%					
Skull length Pmx- condyle				128.6 e	154 e	Type *B. grangeri* 128.6 Size II	
Sk. l. / R				106% e			
P^1–m^3						40.3	
P^2–m^3						38.1	38 Grade II
P_2–m_3	(34.7 e)			38.4			
P_2–m_3 / R				31%			
Lower jaw length inc. to angle	75 e			83	99		
Lower jaw l. / R				69%			

relatively small size of the concave facets for the capitula of the ribs, perhaps indicating less extreme movements of the ribs in respiration.

RIBS

Several ribs (Figs. 20, 21) were found associated with two of the smaller animals (Grade IV), while others (Fig. 22) were found with No. 26166, one of the larger animals (Grade II). Careful comparisons with the ribs of the Indian rhinoceros reveal surprisingly close resemblances, both in general form and in details, so that we were able to determine approximately the serial number of the individual ribs. Dorsal ribs 6, 8, 10, 12, 14 and the first lumbar rib, as well as the various ribs figured by Borissiak, thus prove that the shape of the thorax as a whole was close to that of the Indian rhinoceros. However, on account of the very long radius and femur of *Baluchitherium*, its thorax would look decidedly smaller in proportion to the height of the whole animal.

LIMBS AND FEET

Comparison of *Baluchitherium* limb bones with those of the highly specialized modern rhinoceroses establishes the fact that while *Baluchitherium* has retained surprisingly many characters of the ancestral cursorial rhinoceros, it has also acquired a few "graviportal" characters with its great weight. Of these perhaps the most outstanding are: the lengthening of the femur, the shortening of the tibia, the widening of the astragalus and of the ungual phalanges of the middle digits. On the other hand, the usual shortening of the middle digits is conspicuously absent. In fact *Baluchitherium* alone among gigantic perissodactyls has widened and elongated the middle metapodials and phalanges, especially in the manus.

In the vertebral column the chief graviportal characters are the widening of the neck vertebrae and the deep lateral excavation of the centra.

Our comparative measurements and studies of the skeletons of *Rhinoceros sumatrensis*, *Rhinoceros unicornis* and *Ceratotherium simum* indicate that in the modern rhinoceroses the legs have become relatively short and broad, while the body has increased greatly in bulk; the occiput has broadened as the nasal horns have developed. In *Baluchitherium,* on the other hand, the limbs rapidly lengthened while the head became long and low and remained hornless.

The SCAPULA is best known from Borissiak's specimen (text fig. 2, p. 56), which reveals a rather slender straight spine, a transversely thick, expanded glenoid articular surface and a massive transversely thick process for the tendon of the biceps. The antero-posterior width of the bone is not known but Granger records a field measurement of 80 cm. for the "length" (height) of the scapula in a rather small individual (No. 26387) associated with vertebrae and limb bones. This length would be only 70 per cent of the length of the radius of the same individual, a surprisingly low figure. The shape of the scapula differs very widely in the various genera of fossil and recent rhinoceroses but in those that have very long dorsal spines, as in the white rhinoceros, the scapula, while massive, is greatly elongated vertically. Nevertheless the positive

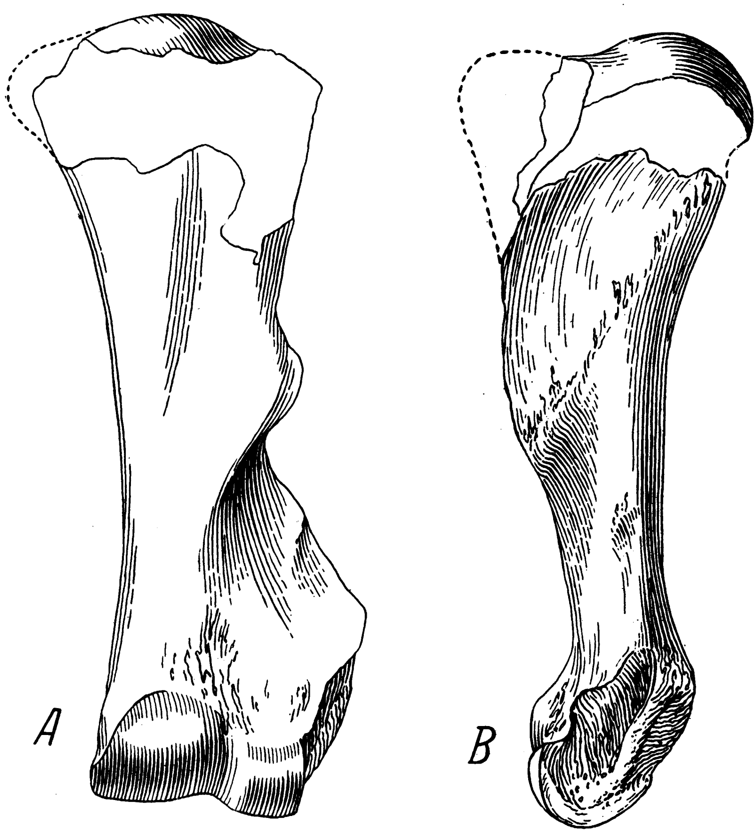


Fig. 23. Left humerus of *Baluchitherium grangeri*. (Large animal, size Grade II, No. 26166.) $\times {}^1/_{10}$ natural size.

A. Anterior view. *B.* Lateral view.

measurement recorded by Granger indicates a relatively short scapula; accordingly we have assigned to this bone in the restoration a contour of generalized rhinocerotic type, somewhat widened antero-posteriorly. Yet the scapula of *Indricotherium* as figured by Borissiak was remarkably thick transversely at the lower end; thus the bone doubtless played its full share both in supporting the huge body through the subscapularis

A B

Fig. 24. Right radius of *Baluchitherium grangeri*. (Large animal, size Grade II, No. 26166.) $\times {}^1/_{10}$ natural size.

A. Anterior view. *B*. Lateral view.

and serratus muscles and in forming part of the fulcrum for the neck and skull through the superficial neck muscles.

The HUMERUS (Fig. 23) is of enormous strength and thickness. Its length, 98.5 cm., in our largest specimen, which is known to belong to an animal of the second size rank (see p. 65), somewhat exceeds the dimensions recorded by Borissiak (pp. 58, 59). The immense, gently convex head faces chiefly upward and less backward than in more typical rhinoceroses. This implies only a gentle inclination of the scapula to the humerus in the standing pose. The prominent deltopectoral crest, triangular in cross-section, stiffens the bone on the anterior face. The

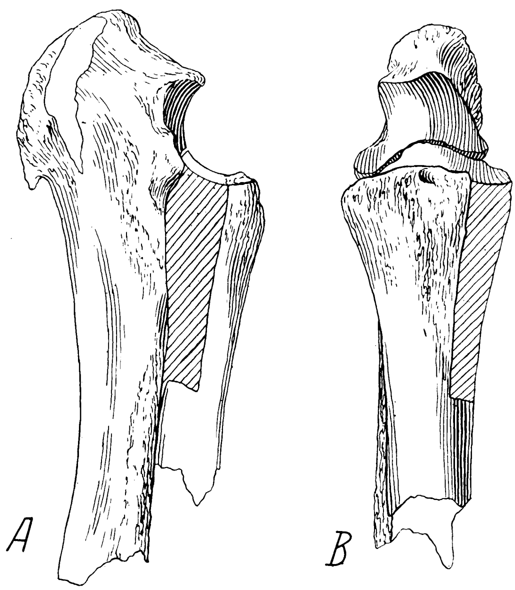


Fig. 25. Part of right radius and ulna of *Baluchitherium grangeri*. (Size Grade IV, No. 26169.) $\times {}^{1}/_{10}$ natural size.
A. Lateral view. *B*. Anterior view.

great tuberosity was almost sessile on top of the deltopectoral crest. The lesser tuberosity is massive but low, implying a powerful subscapularis muscle. Although the bicipital groove was not pronounced, the biceps itself must have been of enormous size, as we know from the great thickness of the bicipital process on the scapula and the prominence of the bicipital eminence on the radius.

The humerus is much shorter than the radius, possibly because *Balu-*

chitherium is a direct descendant of cursorial rhinoceroses, with relatively short humeri and long radii and ulnae. As shown by articulating the humerus with the radius, the angle between the two bones in the standing pose is distinctly greater than in Borissiak's restoration.

The RADIUS (Fig. 24) is a very long bone flattened in front but of massive cross-section, the length reaching 122 cm. in our largest specimen, as compared with 94.5 cm. in *Parelephas imperator*. The distal end is subrectangular in section, which gives great resistance to bending stresses. It is immediately derivable from the cursorial radius of "*Epiaceratherium*" (Borissiak, Tab. II, fig. 3).

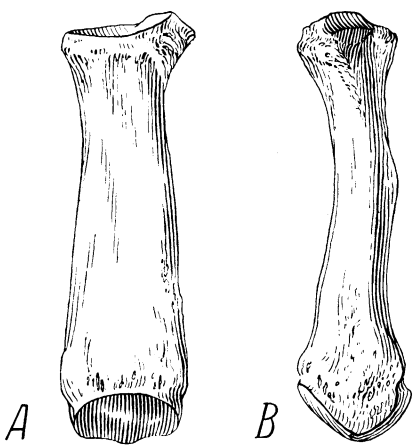


Fig. 26. Third left metacarpal of *Baluchitherium grangeri*. (Large animal, size Grade II, No. 26166.) $\times 1/10$ natural size.
A. Anterior view. *B*. Lateral view.

The ULNA (Figs. 25, 38) is considerably longer than the radius, and has a prominent, well-rounded but not gigantic olecranon and relatively slender shaft.

The MANUS, having been fully described by both Cooper and Borissiak, calls only for the note that one of our third metacarpals (Fig. 45 *F*), attaining an estimated length of 63.5 cm., exceeds any other hitherto recorded. The second largest middle metacarpal (Fig. 26) is fortunately associated with the complete radius and humerus described above. A relatively small and immature manus (No. 21618, Fig. 27) associated with a pes, emphasizes the tendency toward monodactylism already noted by Cooper and Borissiak.

The PELVIS is known chiefly from the specimen figured by Borissiak (p. 91), which according to him was one metre in length. As restored

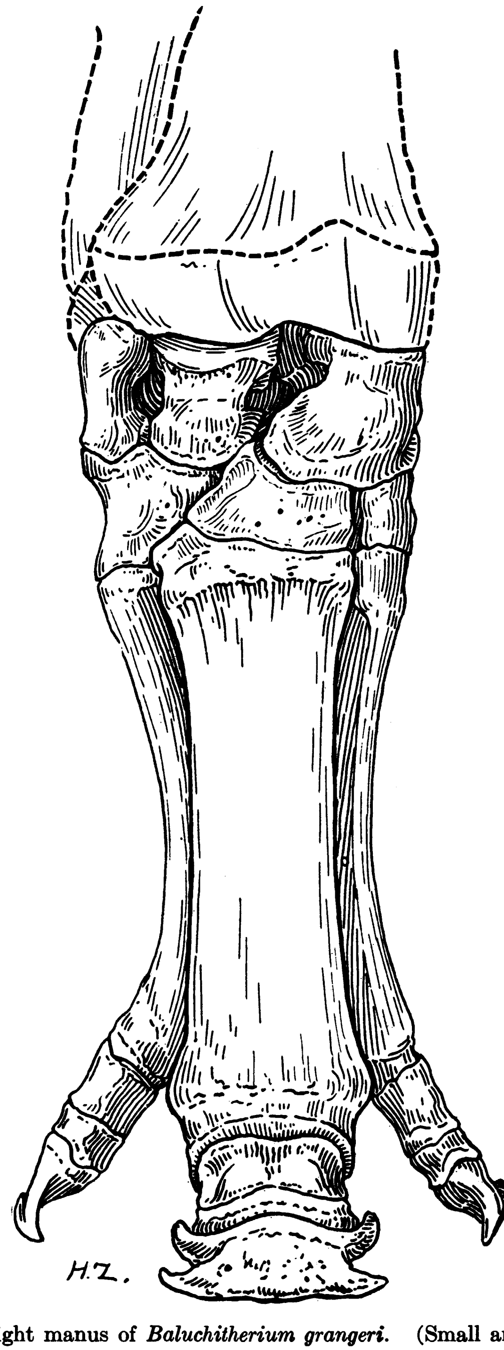


Fig. 27. Right manus of *Baluchitherium grangeri*. (Small animal, size Grade IV, No. 21618.) ×1/5 natural size.

the dorsal crest of the ilium was not expanded in the usual way among gigantic animals. Since, however, Borissiak's figure shows that the blade of the ilium was badly broken in small pieces, it raises a doubt whether the dorsal border is correctly restored. Moreover, a pelvis of a very large ungulate provisionally referred to *Baluchitherium* was photographed by Forster Cooper (1923, p. 371, Fig. 2) in the field.

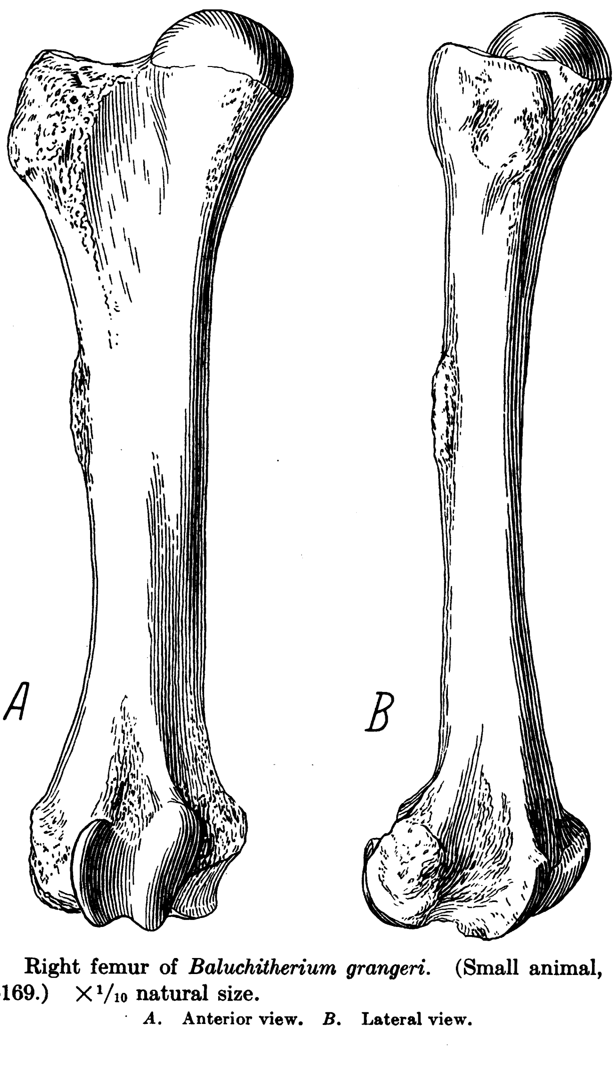


Fig. 28. Right femur of *Baluchitherium grangeri*. (Small animal, size Grade IV, No. 26169.) $\times {}^{1}/_{10}$ natural size.

A. Anterior view. *B*. Lateral view.

This specimen has the widely expanded dorsal crest of the ilium as in other large rhinoceroses. Accordingly in our restoration (Fig. 47) we have given the pelvis an expanded dorsal crest. Nor can we agree with Borissiak in giving the pelvis such a nearly vertical position in the restoration of the skeleton, since the characters of the sacrum indicate that the inclination of the ilium to the backbone was not essentially different from that which is found in other rhinoceroses.

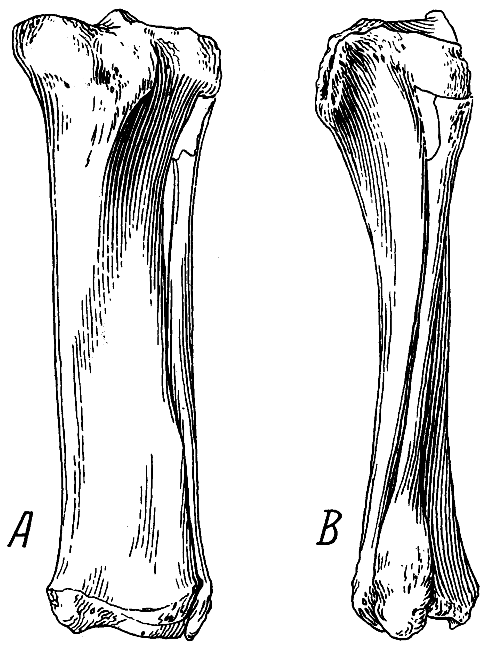


Fig. 29. Left tibia and fibula of *Baluchitherium grangeri*. (Small animal, size Grade IV, No. 26169.) $\times {}^{1}/_{10}$ natural size.
A. Anterior view. *B*. Lateral view.

Granger records a field measurement of a pelvis of 112 cm. length associated with a radius of the same length and a femur of 128.5 cm. length. If we multiply the length of Granger's pelvis by 1.4 (the factor used to enlarge size IV to size I) it makes an estimated length of 156.8 cm. In our restoration of size I we have somewhat exceeded this estimate, but such an immense hind limb of distinctly rhinocerotic type would seem to require a large ilium with a spreading crest, especially

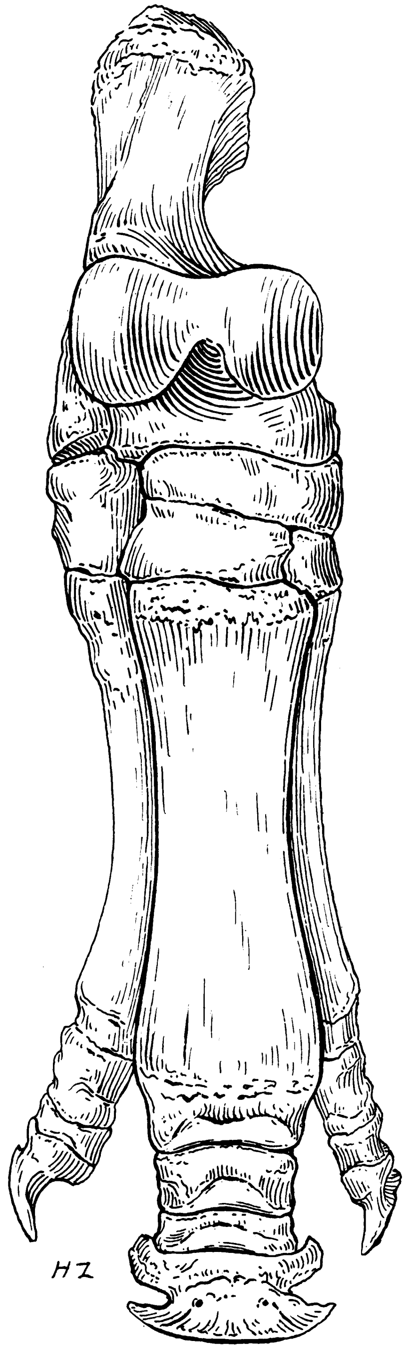


Fig. 30. Right pes of *Baluchitherium grangeri*. (Small animal, size Grade IV, No. 21618.) $\times {}^1/_5$ natural size.

since the ribs and vertebrae indicate a thorax and lumbar region closely approaching those of *Rhinoceros indicus*.

The FEMUR (Figs. 28, 41) is represented by several good specimens in our collection, which show that the third trochanter is far less reduced than one would suppose from Borissiak's text figure 10, page 93. The great trochanter lies well below the level of the head. We cannot agree with Borissiak in making the shaft of the femur almost vertical in the restoration, as a direct fitting of associated bones shows that the knee was bent even in the standing pose.

The TIBIA (Fig. 29), remarkably short and wide, is beautifully preserved in one specimen, associated with femur and fibula. Both field and laboratory measurements indicate that the tibia is about 66 per cent

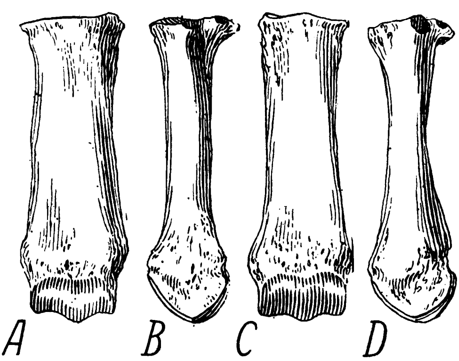


Fig. 31. Middle metatarsals of *Baluchitherium grangeri*. (Small animals, size Grade IV.) $\times {}^1/_{10}$.

A. Right, anterior view, No. 26387. *C*. Left, anterior view, No. 26169.
B. Right, inner view, No. 26387. *D*. Left, lateral outer view, No. 26169.

of the length of the femur and is thus rather graviportal in proportions. The rectangular cross-section of its lower end is well adapted to resist the great bending stresses to which this bone was subjected.

The FIBULA (Fig. 29) is well preserved in two of the smaller specimens. It has a slender shaft and expanded distal end.

The PES (Fig. 30), having been fully described by Borissiak, requires little comment except that even in our somewhat immature specimen the tendency toward monodactyly is pronounced. The middle metatarsal (Fig. 31), preserved in two of the smaller specimens, is slightly shorter and relatively stouter than the middle metacarpal. In spite of the graviportal adaptations of the astragalus (Fig. 32), the cuboid facet of that

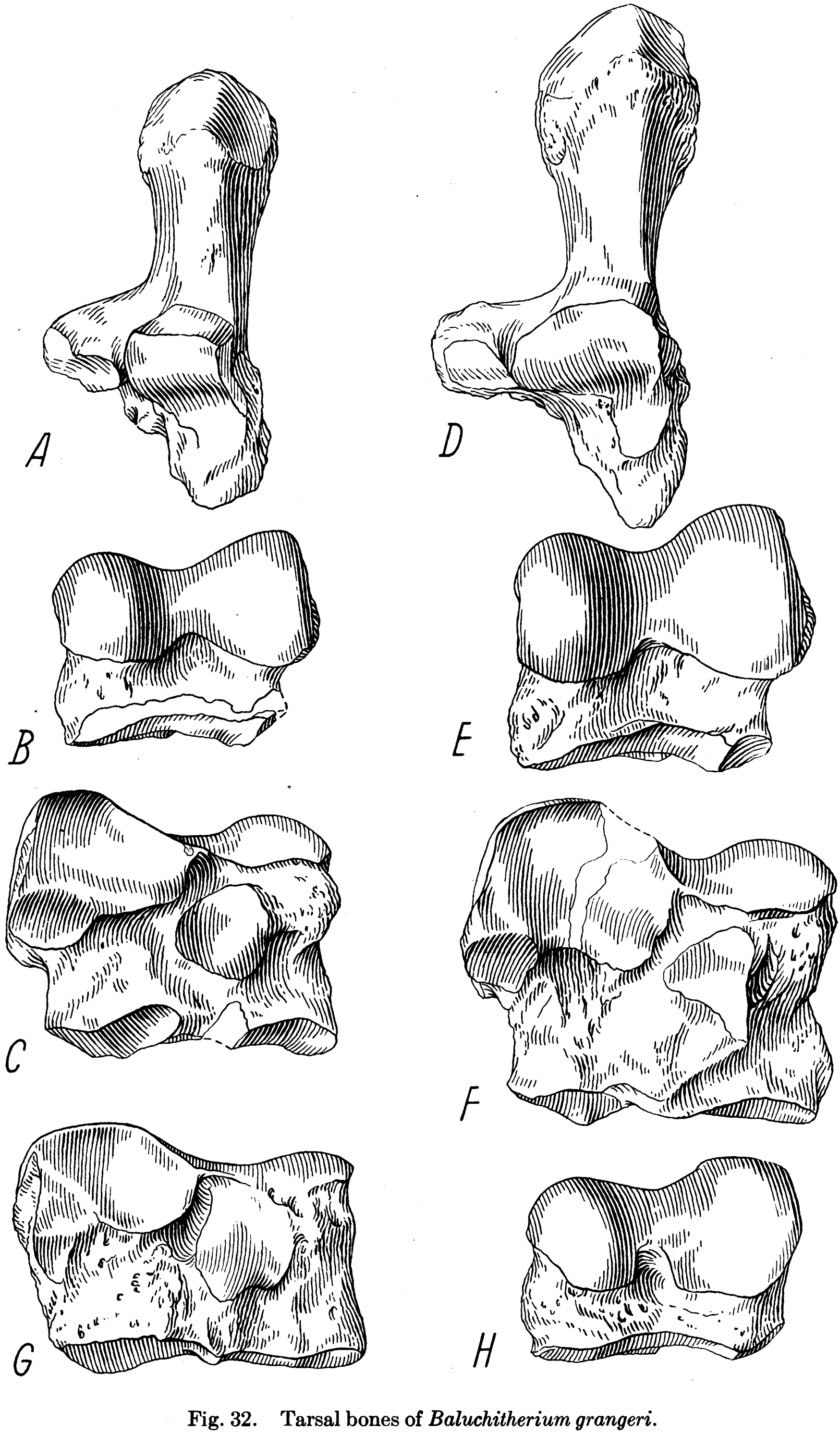


Fig. 32. Tarsal bones of *Baluchitherium grangeri*.

A. Left calcaneum, anterior view, No. 26387. × 1/5.
B. Left astragalus, anterior view, No. 26387. × 1/5.
C. Left astragalus, posterior view, No. 26387. × 1/4.
D. Left calcaneum, anterior view, No. 26973. × 1/5.
E. Left astragalus, anterior view, No. 26973. × 1/5.
F. Left astragalus, posterior view, No. 26973. × 1/4.
G. Left astragalus, posterior view, No. 5209. × 1/4.
H. Left astragalus, anterior view, No. 5209. × 1/5.

bone is but little increased, in contrast to the conditions observed in the graviportal titanotheres.

The associated FORE AND HIND FEET (Figs. 27, 30) of a single articulated skeleton, the rest of which had been unfortunately eroded away, give us some valuable correlations of measurements between the manus and pes, and since the limbs of the animal were preserved nearly *in situ*, they also afford an approximation to the distance between the fore and hind limbs. On the right side the distance between centers of the fore and hind feet was 229 cm., on the left, 254 cm., giving an average distance between fore and hind feet of 241 cm. As the legs were directed outward in the death pose, the distance between the two hind feet (152 cm.) is of little value. Other measurements of this small and somewhat immature specimen are given in Table VIII.

TABLE VIII.—MEASUREMENTS OF ASSOCIATED FORE AND HIND FEET (No. 21618)

Radius, transverse distal end	25.5	Mtc. III, r. length	40–42
Carpus, transverse proximal end	23.5	Mtc. III, width prox.	13.5
Carpus, mid. height	16	Mtc. III, max. width dist.	14
Carpus, lateral height		Width dist. phal. Mtc. III	14
Carpus, height cun. + unc.	17.5	Width prox. " " "	12.5
Distance between centers, right fore foot and right hind foot	229	Mtc. III, l. length	40–42
		Mtc. III width, prox.	
Distance between centers, left fore foot and left hind foot	254	Mtc. III max. width dist.	
		Mtc. II, length	36.5
Average distance	241	Mtc. II, width	
Width between fore feet	135	Mtc. IV, length	35
Width between hind feet (sprawled)	152	Tibia, width dist. end	19
Average distance	143	Tarsus, height, front (tibia to prox. Mts. III)	16

	No. 21618	No. 26387	No. 21619
Mts. III, r. length	39	40	
Mts. III, width, prox.	12	14	
Mts. III, width, distal	12	15	
Max. width, Phal. III			14
Width, prox. " "			14
Mts. II, length	33		
Mts. IV, length	32		
Calcaneum, length	26.5	28	
Astragalus, width across condyle	16.5	17.3	

To sum up with regard to the proportional lengths of the segments of

TABLE IX.—COMPARATIVE LIMB MEASUREMENTS OF *Baluchitherium*

	Small *Baluchitherium* Grade IV	Large *Baluchitherium* Grade II	*Allacerops turgaicum* ("*Epiaceratherium*")	*Trigonias osborni*	*Rhinoceros sumatrensis*	*Equus caballus* (cursorial)	*Brontops robustus*	*Mastodon americanus*
Scapula, length	80		30	31	35.8			
Humerus, length	90 e	98.5	33.2	27	36.8			
Scapulo-humeral index $\frac{S}{H}$	88% e		90%	90% e	97%	120%	123%	93%
Humerus, length	90 e	98.5	33.2	27	36.8			
Radius, length (outer side)	112	122	29.6	25.5	27.5			
Radio-humeral index $\frac{R}{H}$	123%	124%	112%	95%	75%	119%	82%	75%
Metacarpal III, length	44	53.5	14.7	12	14.4			
Metacarpo-humeral index $\frac{\text{Mtc. III}}{H}$		54.5%	44%	45%	39%	78%	37%	18%
Pelvis, length	112	122 e	42	41	47.5			
Femur, length (head to ext. cond.)	128.5	139 e	36.8	33	43.7			
Pelvi-femoral index $\frac{\text{Plv}}{F}$	87%(?)		116%	128%	108%			
Tibia, length	84	92 e	24.6	25	27.3			
Tibio-femoral index $\frac{T}{F}$	66%	66% e	67%	76%	62%	92%	55%	69%
Metatarsal III	40	50	15	11	13.3			
Metatarso-femoral index $\frac{\text{Mts. III}}{F}$	31%	36% e	43%	33%	30%	73%	26%	11%

the limb bones in *Baluchitherium*, we may note the following striking results recorded in Table IX:

(1) *Allacerops* ("*Epiaceratherium*") in most of its limb segment ratios tends either to be intermediate between *Trigonias* and *Baluchitherium* or to agree with either one or the other.

(2) In *Baluchitherium* the scapula is relatively very short, as compared with the humerus, whereas in the cursorial *Equus* the scapula is long.

(3) In *Baluchitherium* the radius is very long, both relatively and absolutely.

(4) The middle metacarpal of *Baluchitherium* has shared to some extent in the elongation of the lower half of the fore limb.

(5) The pelvis is relatively short and, conversely, the femur very long.

(6) The tibia and third metatarsal are relatively shorter than the radius and the third metacarpal, respectively.

(7) *Baluchitherium* by this showing belongs among neither the cursorial nor the graviportal types of Osborn, except in certain features (e.g., graviportal ratio of tibia to femur). It is, on the other hand, a gigantic, long-limbed rhinoceros, the ratios of its limb segments being most easily derivable from those of primitive subcursorial ancestors allied with *Allacerops* and *Trigonias*.

RELATIONSHIPS

As to generic relationships, our material indicates that both *Baluchitherium* and *Indricotherium* are close to or even synonymous with *Para-*

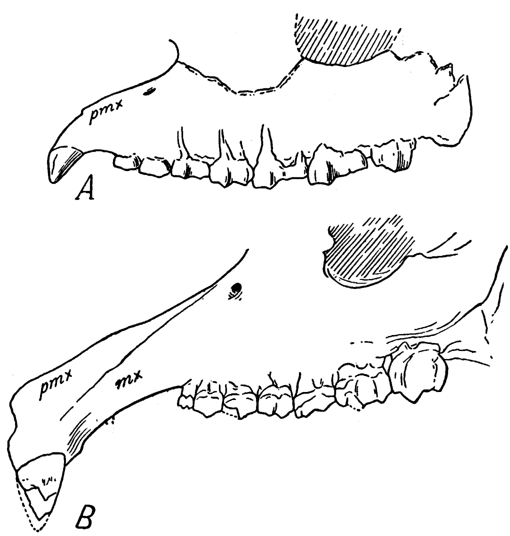


Fig. 33. Left maxilla and premaxilla with teeth.
A. *Epiaceratherium turgaicum.* After Borissiak. $\times 1/6$.
B. *Baluchitherium grangeri.* After Osborn. $\times 1/12$.

ceratherium, although possibly representing slightly different species. In the first place, the type upper molars of *Paraceratherium bugtiense* Pilgrim exhibit no conspicuous differences from those of *Baluchitherium osborni;* secondly, the lower jaw referred to *Paraceratherium bugtiense* by Forster Cooper seems to us to be indistinguishable in generic characters from one of our jaws (No. 26166) that is associated with humerus, radius, ulna and metacarpal III of the general size and characters of Borissiak's *Indricotherium;* thirdly, the cast of the skull referred by

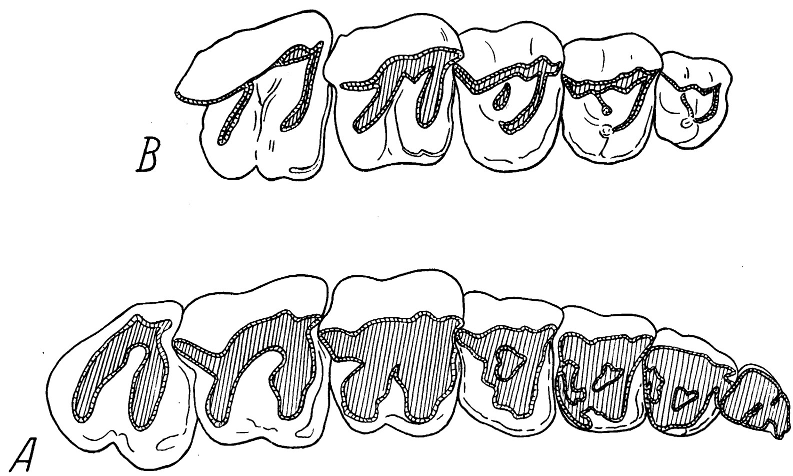


Fig. 34. Right upper cheek teeth.

A. Epiaceratherium turgaicum. After Borissiak. $\times \frac{107.8}{200}$.

B. Indricotherium asiaticum. After Borissiak. $\times \frac{45}{200}$.

Forster Cooper to *Paraceratherium* reveals essential similarities at all points to our large skulls of *Baluchitherium grangeri* Osborn. Unfortunately, however, this substantial identity is obscured by the fact that the *Paraceratherium* skull is crushed vertically and its rostrum is broken off. Fourthly, the peculiar lower front teeth of *Paraceratherium* are matched precisely in *Baluchitherium osborni* and in Borissiak's *Indricotherium.* Fifthly, we have numerous fully adult limb bones, astragali and metapodials that collectively comprise a closely graded series (Figs. 44, 45) from the small *Paraceratherium* through *Baluchitherium osborni* to *B. grangeri* and finally to a super-*Indricotherium*. On the other hand, Borissiak has pointed out that in Forster Cooper's *Paraceratherium* the protoloph of the fourth upper premolar is higher than in *Indricotherium*, the whole crown is slightly more hypsodont and the cingulum better developed; also the incipient "crochets" of the upper molars are a little

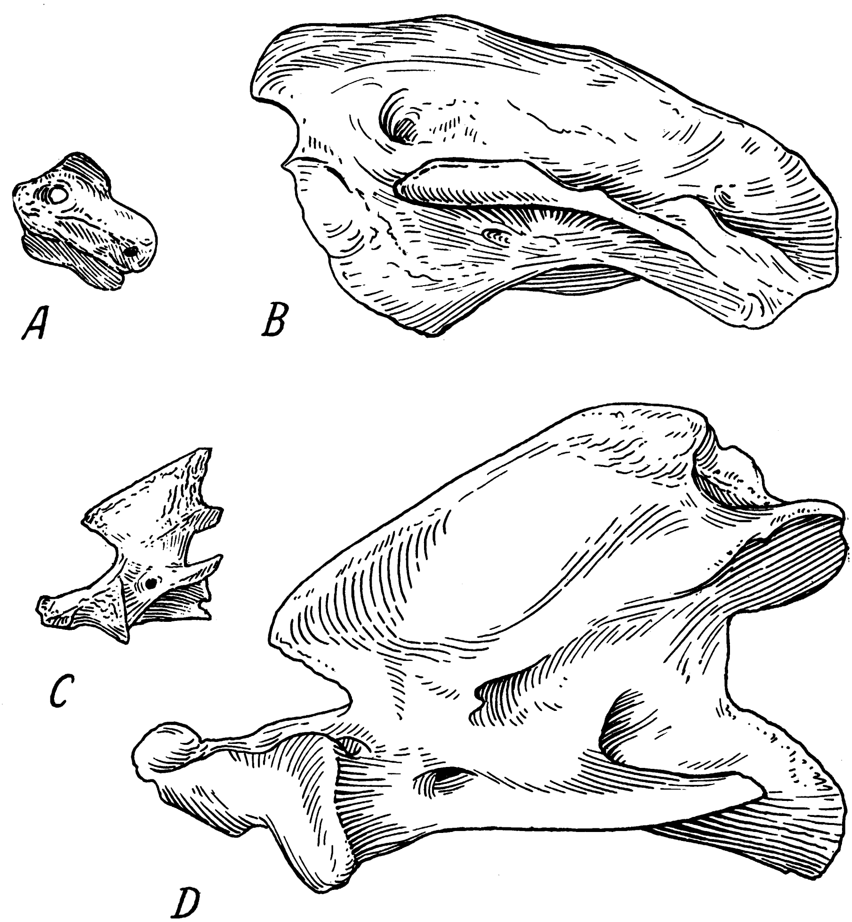


Fig. 35. Atlas and axis. $\times ^1/_5$.
A, C. Epiaceratherium. After Borissiak.
B, D. Baluchitherium.

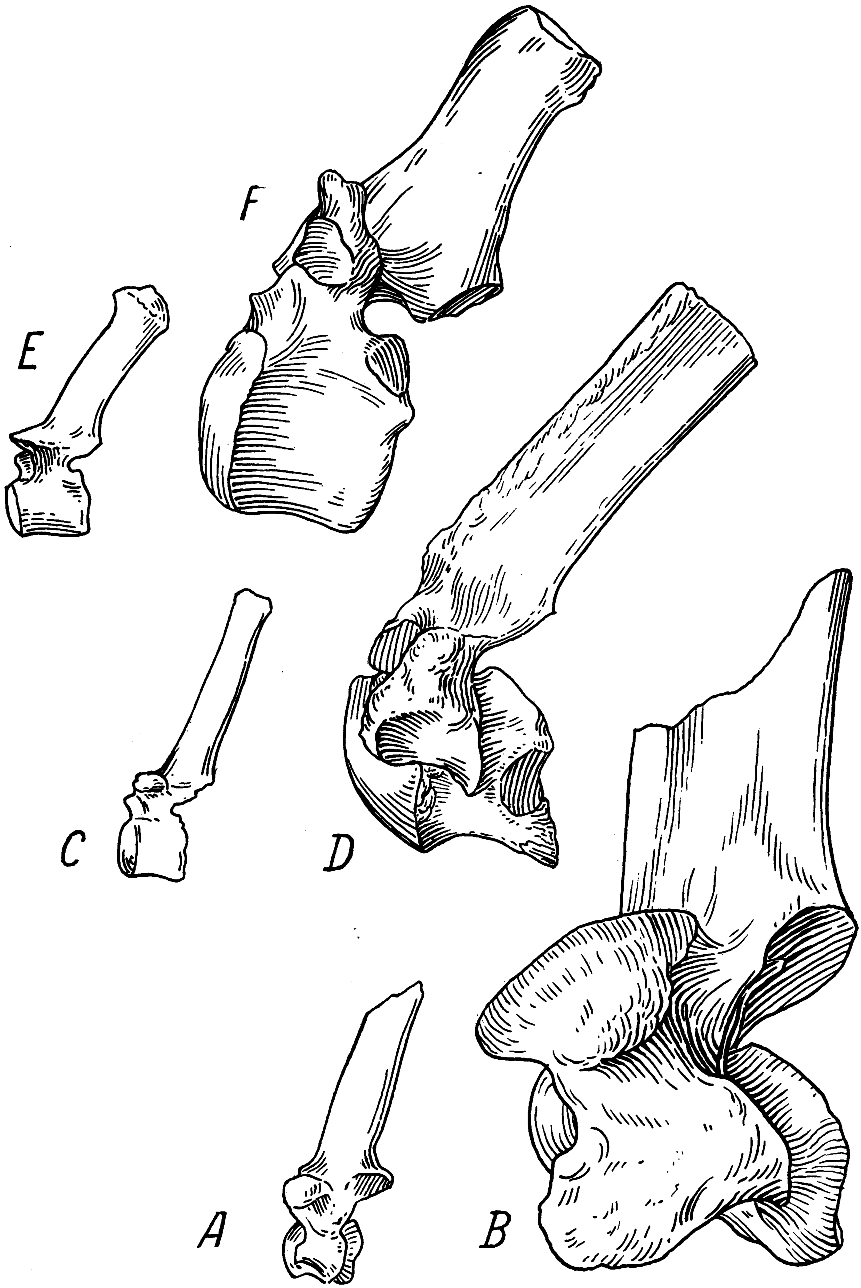


Fig. 36. Dorsal vertebrae. $\times{}^{1}/_{5}$.

A. First (?) dorsal of *Epiaceratherium*. After Borissiak.
B. First dorsal of *Baluchitherium*.
C. Fourth (?) dorsal of *Epiaceratherium*. After Borissiak.
D. Fourth dorsal of *Baluchitherium*.
E. Fourteenth (?) dorsal of *Epiaceratherium*. After Borissiak.
F. Thirteenth dorsal of *Baluchitherium*.

more pronounced; assuredly, however, the evidence assembled in Fig. 2 above is not favorable to the idea that *Paraceratherium, Baluchitherium* and *Indricotherium* are distinct genera, although there are minor and perhaps specific differences, especially in the second upper premolars. Moreover, our experience with the remarkable variability of Oligocene

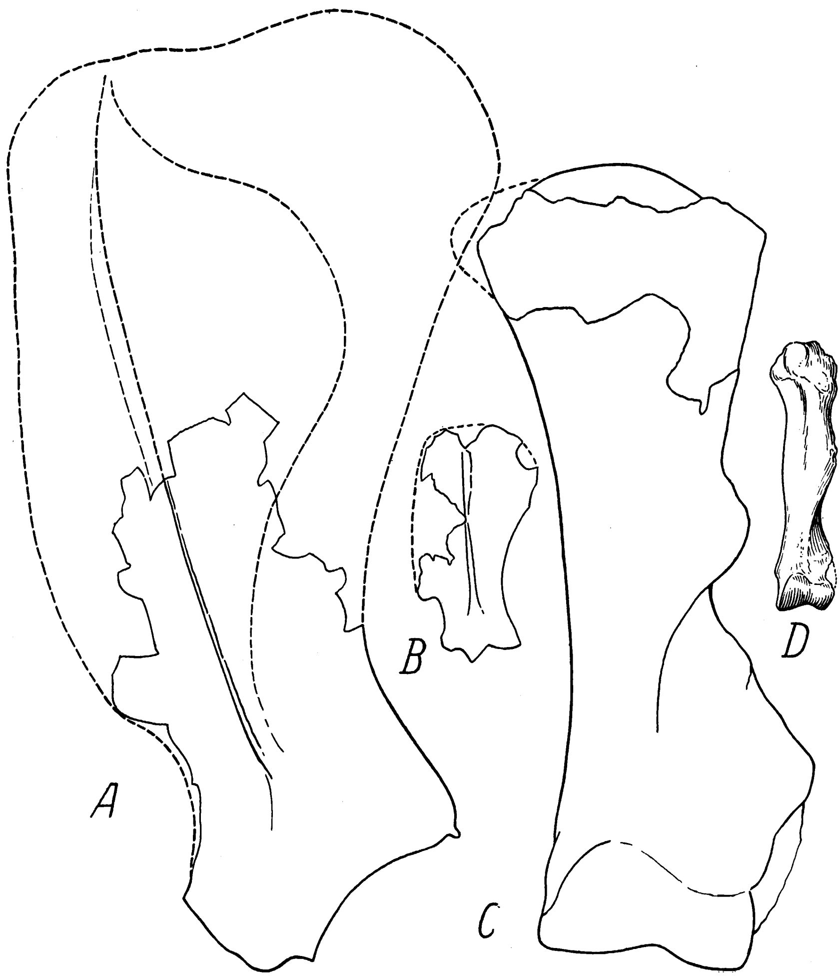


Fig. 37. Left scapula and left humerus. $\times {}^{1}/_{5}$.

A. Scapula of *Indricotherium*. After Borissiak but outline restored and enlarged to size Grade I.
B. Scapula of *Epiaceratherium*. After Borissiak.
C. Left humerus of *Baluchitherium*. Anterior view.
D. Left humerus of *Epiaceratherium*. Anterior view. After Borissiak.

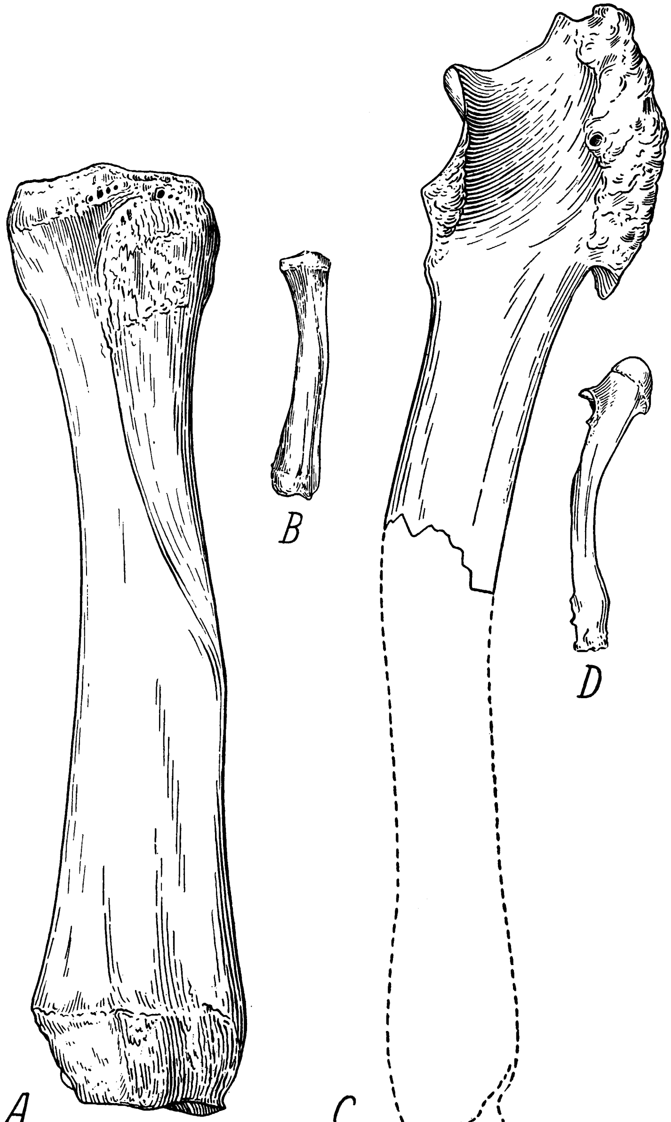


Fig. 38. Right radius, left ulna. $\times {}^{1}/_{10}$.

A. *Baluchitherium grangeri.*
B. *Epiaceratherium.* After Borissiak.
C. *Baluchitherium grangeri.*
D. *Epiaceratherium.* After Borissiak.

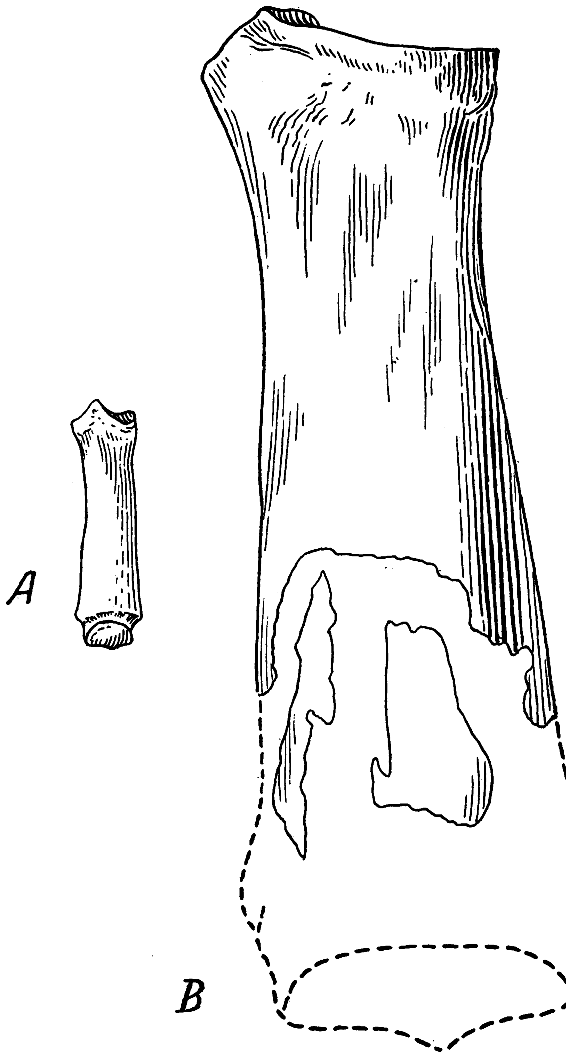


Fig. 39. Right third metacarpal. ×$^1/_5$.
A. *Epiaceratherium*. After Borissiak.
B. *Baluchitherium* (size Grade I).

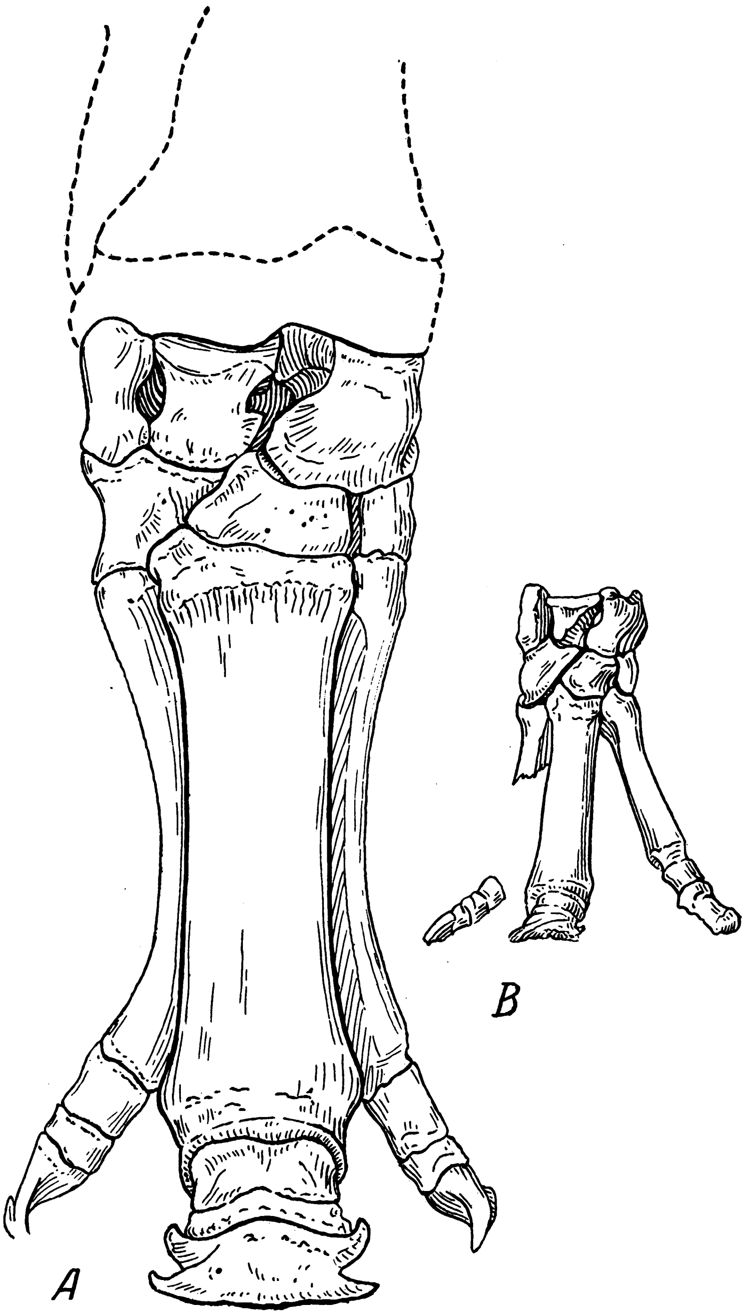


Fig. 40. Right manus. $\times {}^1/_5$.
A. Baluchitherium grangeri (immature).
B. Epiaceratherium. After Borissiak.

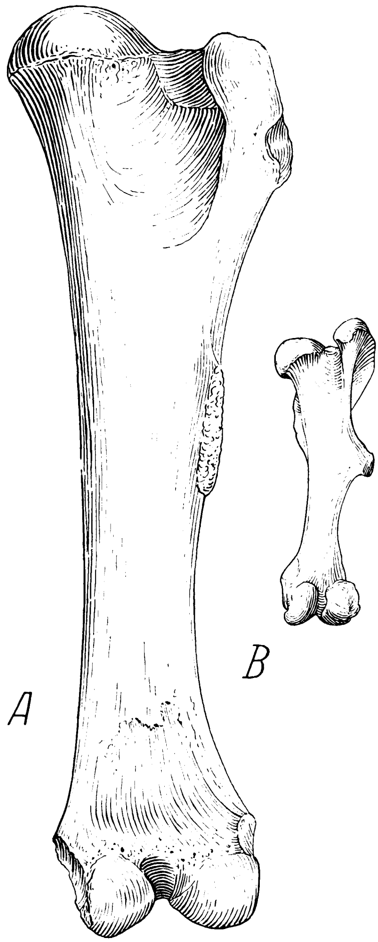


Fig. 41. Right femur, posterior surface. $\times \frac{1}{10}$.
A. *Baluchitherium grangeri* (size Grade IV).
B. *Epiaceratherium*. After Borissiak.

rhinoceros premolars would make us hesitate to allow a superspecific value to such differences.[1] We accordingly continue to use the name *Baluchitherium grangeri* Osborn for the Mongolian material.

As noted by Matthew, the type of *Baluchitherium mongoliense* Osborn (1924) from the Loh formation, ? Lower Miocene, represents a far more advanced type of rhinocerotid, with submolariform p^4 and com-

[1] Cf. Gregory and Cook, 'New Material for the Study of Evolution: A Series of Primitive Rhinoceros Skulls (*Trigonias*) from the Lower Oligocene of Colorado.' Proc. Colorado Mus. Nat. Hist., VIII, No. 1, February, 1928.

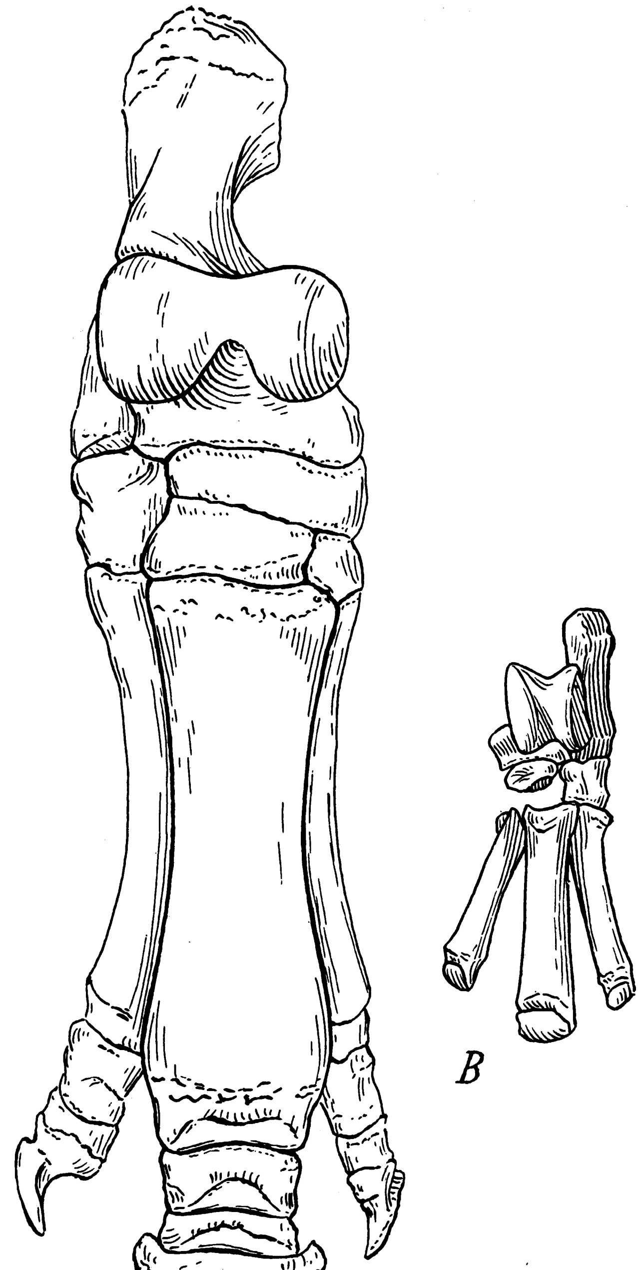


Fig. 42. Right pes. $\times {}^1/_5$.
A. *Baluchitherium grangeri* (size Grade IV).
B. *Epiaceratherium*. After Borissiak.

plex hyposodont molars. It appears to belong to a very different subfamily of rhinoceroses from *Baluchitherium*.

As to the derivation of *Baluchitherium* from more primitive hornless rhinoceroses, Borissiak in his memoir on "*Epiaceratherium turgaicum*" (a small light-limbed rhinoceros contemporary with *Baluchitherium*) has remarked (1918, p. 82) that *Epiaceratherium* is morphologically related to the primitive *Aceratherium* and that all the differences between it and *Indricotherium*, although so marked, even apart from size, in the form of

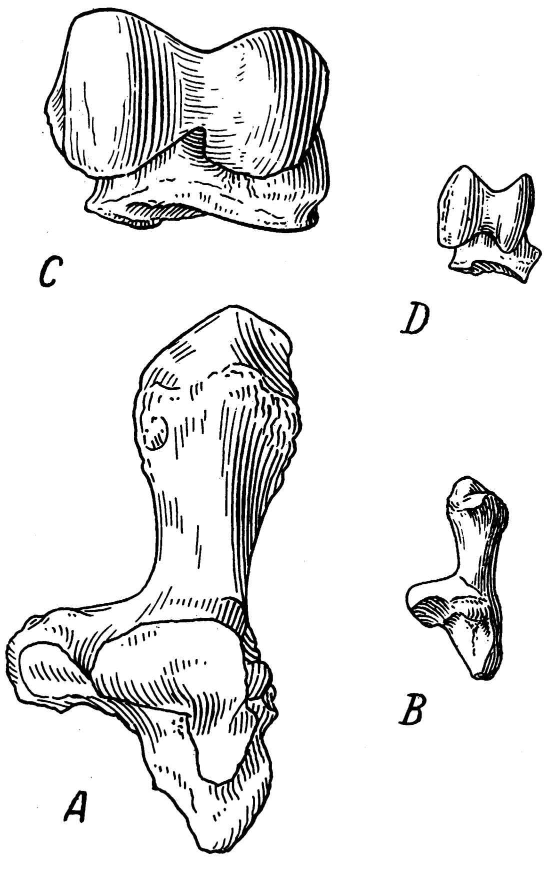


Fig. 43. Right astragalus and left calcaneum. $\times \frac{1}{5}$.

A. *Baluchitherium grangeri.*
B. *Epiaceratherium.* After Borissiak.
C. *Baluchitherium grangeri.*
D. *Epiaceratherium.* After Borissiak.

the bones and of their articular surfaces, ought to be attributed to the unique specialization of *Indricotherium*. After comparing Borissiak's excellent figures of the teeth and bones of "*Epiaceratherium*" (= *Allacerops*[1]) with those of *Baluchitherium* and *Indricotherium*, we would go even farther than he does and say that in regard to its vertebrae and limb bones this small subcursorial rhinoceros (Figs. 33–43) makes an ideal *structural ancestor* for its huge contemporary. The accompanying table (Table IX) of limb measurements and limb ratios suggests that "*Epiaceratherium*" (= *Allacerops*) affords an intermediate structural stage connecting *Baluchitherium* with more primitive ancestors typified by *Eotrigonias* Wood.

RESTORATION

The principal parts of the skeleton, except the sternebrae, are represented in the collection. As noted above, there is an enormous range in the size of the adults, the smallest middle metacarpal of the manus (Figs. 44, 45) measuring 405 mm., the longest, 635 mm. in length. We have grouped the material used in the restoration under four descending grades of size. The middle metacarpal of Grade I is about 1.4 times as long as that of Grade IV, 1.3 times that of Grade III and 1.2 times that of Grade II. Consequently these factors, along with others, have been used (Fig. 46) in enlarging bones of the smaller grades to the probable size of Grade I, which is represented by several gigantic cervical vertebrae and by the third metacarpal. Grade II includes the huge skull, a lower jaw associated with a humerus, radius and middle metacarpal, and several ribs (Amer. Mus. No. 26166). Grade III is represented by the smaller occiput, atlas, axis. Grade IV includes associated manus and pes and various associated vertebrae, ribs, femur, tibia and middle metatarsal. Those who are familiar with the difficulties in securing consistent consecutive measurements from large fossil bones that are more or less imperfect or distorted will not expect our work to be free from errors.

After repeated revisions our restoration (Fig. 47) represents an animal of the largest grade, seventeen feet, three inches in height at the shoulder (top of spine at first dorsal vertebra). The height at the shoulder as thus estimated exceeds that of the tallest hitherto known land mammal.[2] Estimated length (Grade I) in standing pose, from tip of

[1] Dal Piaz (1930) has shown that "*Epiaceratherium turgaicum*" Borissiak is not congeneric with *E. bolcense*, the genotype, and H. E. Wood, 2d. (1932), has made Borissiak's species the genotype of *Allacerops*.

[2] With the possible exception of the Upper Miocene *Dinotherium giganteum*, to which M. Boule (1935, p. 610) assigns a possible maximum height of 5 meters.

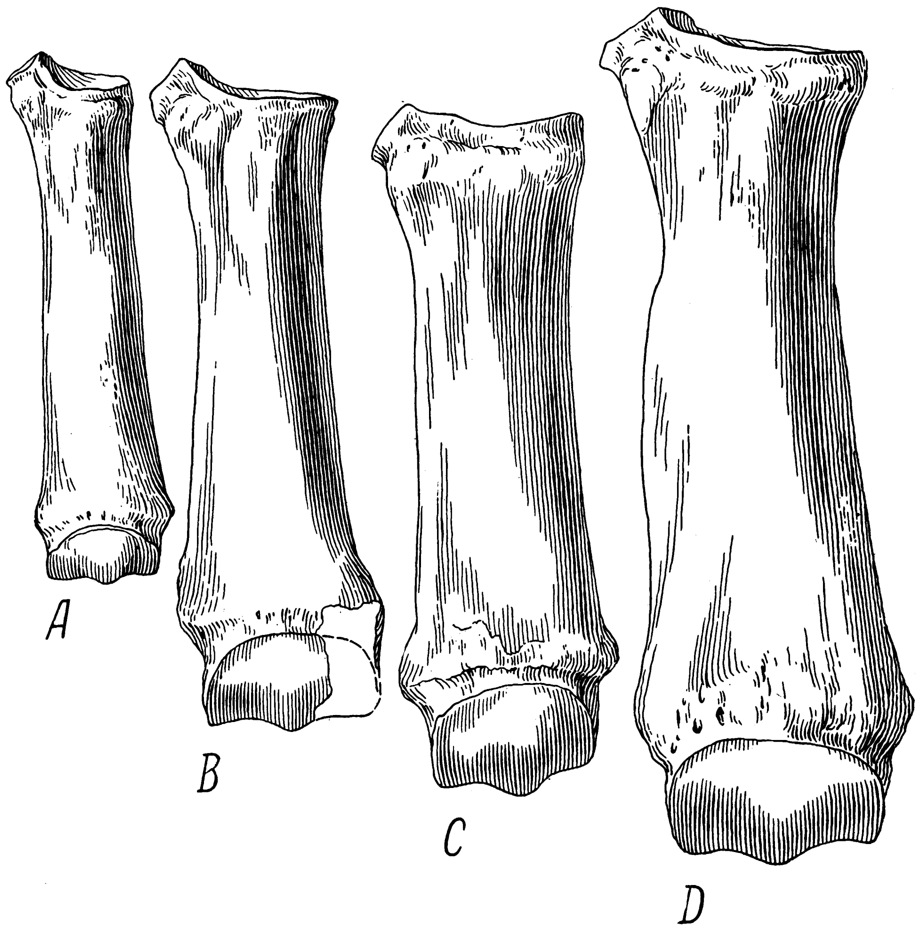


Fig. 44. Right third metacarpals. $\times 1/5$.

A. ? *Paraceratherium* sp., No. 26190 (extremely small).
B. *Baluchitherium grangeri,* No. 26389.
C. *Baluchitherium grangeri.* No. 21618 (size Grade IV).
D. *Baluchitherium grangeri,* No. 26166 (size Grade II).

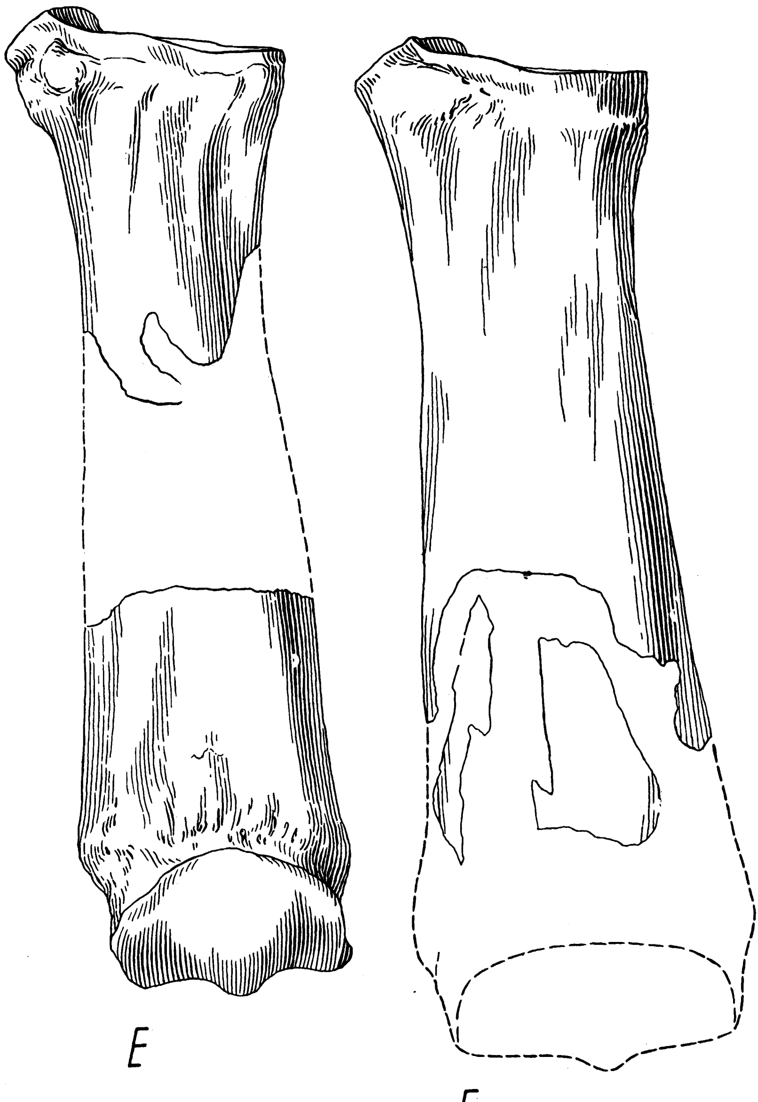


Fig. 45. Right third metacarpals (continued). $\times 1/5$.

E. Indricotherium asiaticum, No. 26973. Cast; original in Moscow. (Size between Grades I and II.)
F. Baluchitherium grangeri, No. 26175. (Size Grade I.)

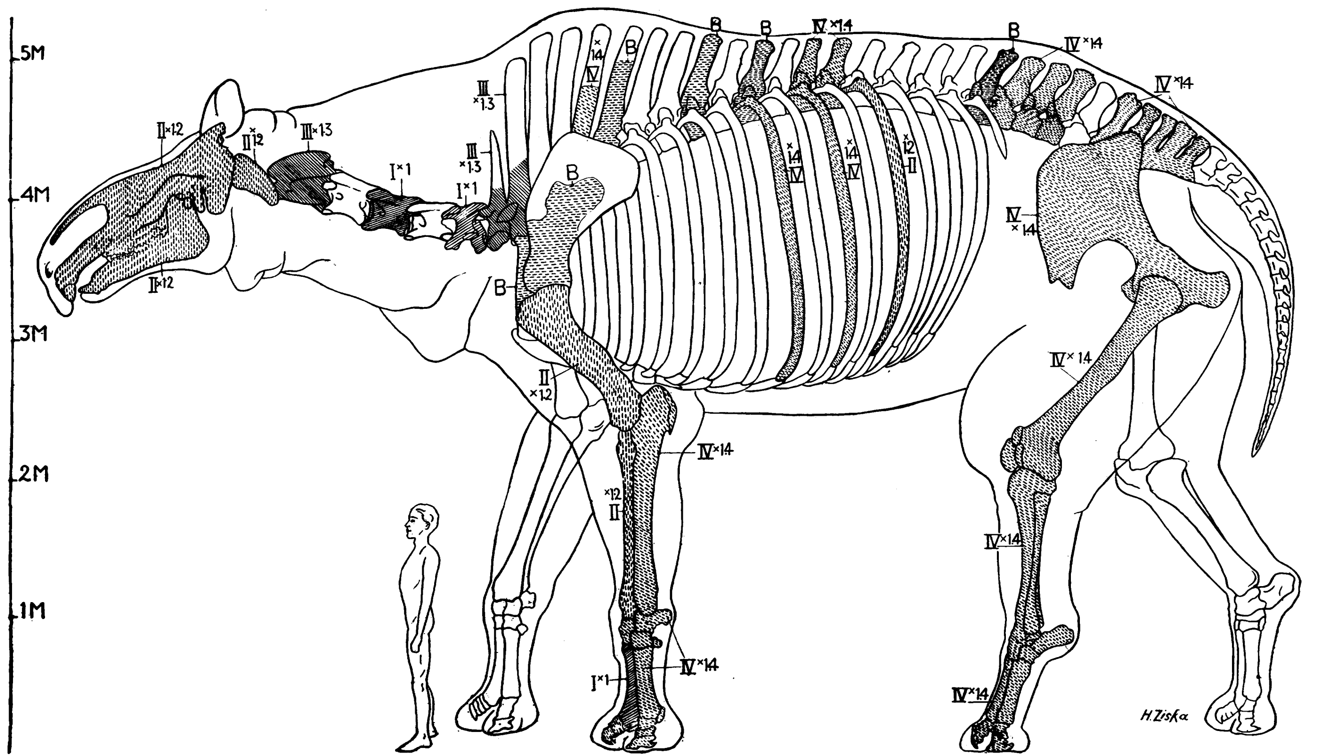


Fig. 46. Restoration of *Baluchitherium*, indicating, by differential shading, the parts belonging to animals of the four grades of size—Grade I being of maximum and Grade IV of minimum size. Bones marked B are from the Borissiak collection.

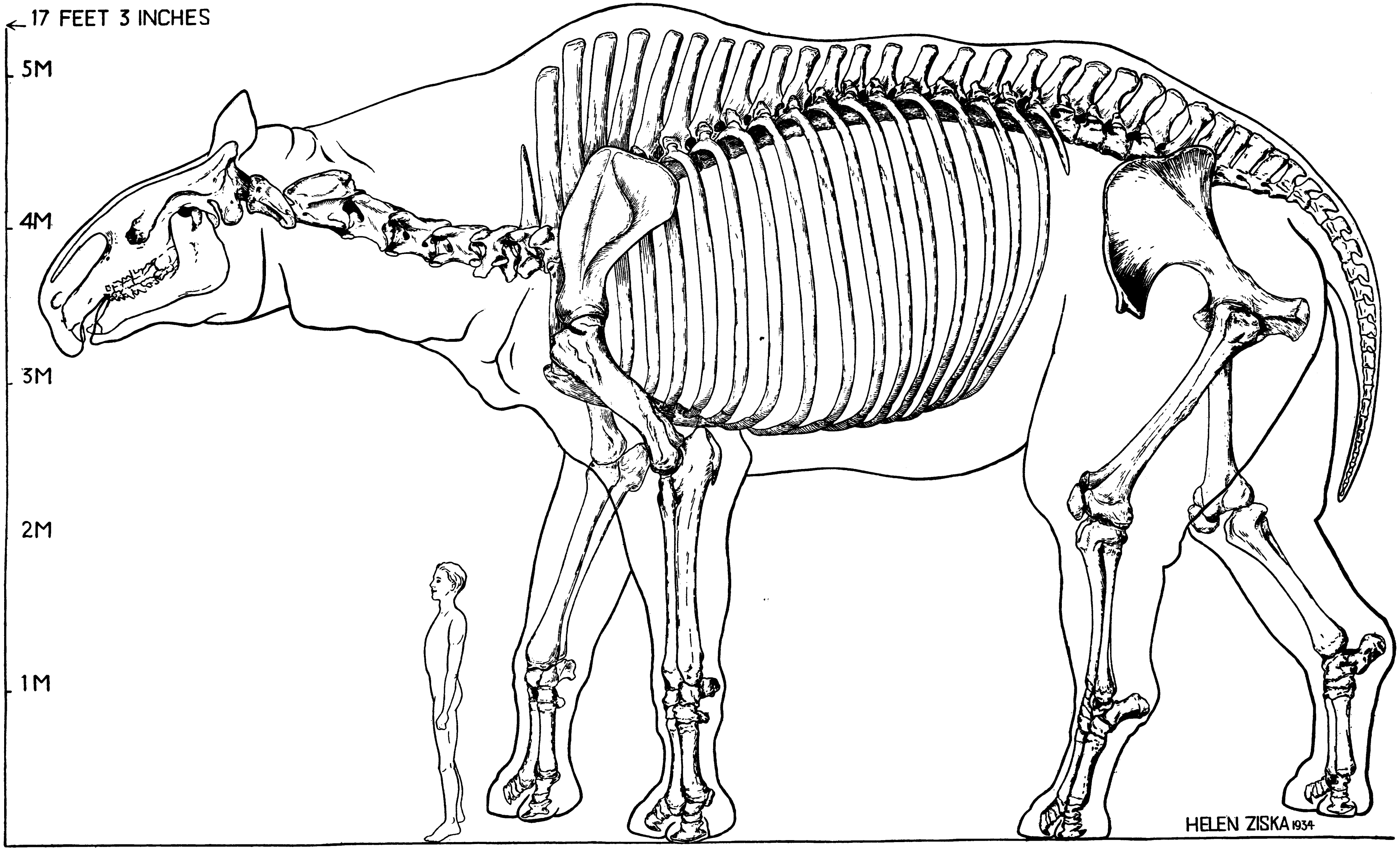


Fig. 47. Revised restoration of *Baluchitherium*. Based upon all available material and drawn to the size of the largest individual represented in the American Museum collection. A six-foot man is drawn to scale for comparison.

premaxilla to ischial tuberosity, about twenty-seven feet. Size Grade II animals would be about fourteen feet at the shoulder, size Grade IV about twelve feet. The skull is relatively small; the axis is comparatively long and low but cervicals 4–7 are relatively very broad and low as compared with those of recent rhinoceroses.

On the whole, our restoration makes *Baluchitherium* not unlike one of the primitive hornless Oligocene rhinoceroses, except for its titanic size and relatively long radius, long femur, small head, elongate axis and wider mid-cervicals. This is also to be inferred from the detailed characters of the individual bones. We can find no evidence for the okapi-like restorations by earlier authors.

LIST OF SPECIMENS OF *BALUCHITHERIUM* AND RELATED FORMS FROM MONGOLIA, 1922–1930

Baron Sog and Houldjin Beds

26165	Posterior half of skull—no teeth.	Urtyn Obo, 1928.
26167	Posterior half of skull—no teeth.	Urtyn Obo, 1928.
26172	Lower jaws, P_2–M_3 right and left.	Nom Kong Obo (Holy Mesa), 1928.
26171	Lower jaw fragment with four cheek teeth.	Urtyn Obo, 1928.
26166	Humerus, left; radius, right; metacarpal III, left; two ribs (D6, D7 ?); lower jaw, right ramus complete and P_{2-4} left. Size Grade II.	Urtyn Obo, 1928.
26169	Distal portion of humerus, left; femur, right; distal half of left femur; tibia and fibula, left; proximal ends of right ulna and radius and left radius and distal ends of both ulnae. Metatarsal III, left; 3d dorsal vertebra and two ribs (D12, 14, right). Size Grade IV.	Nom Kong Obo (Holy Mesa), 1928.
26387	Sacrum, three lumbar and two dorsal vertebrae; left astragalus; astragalus, calcaneum, cuboid, ectocuneiform and metatarsal III of right pes; two proximal and two ungual phalanges of median digit; two ribs (D8 left, D10 left); fibula; patella. Also measured *in situ* but not collected, a femur, scapula, radius and pelvis. Size Grade IV.	25 miles S. W. of Iren Dabasu, 1930.
26168	Two cervical vertebrae—C3 and C6 (association uncertain).	Nom Kong Obo (Holy Mesa), 1928.
26173	Anterior dorsal vertebra.	Urtyn Obo, 1928.
26390	Axis vertebra.	25 miles S. W. of Iren Dabasu, 1930.
26392	Seventh cervical vertebra. Size Grade III.	25 miles S. W. of Iren Dabasu, 1930.
26393	Femur, left.	25 miles S. W. of Iren Dabasu, 1930.
26175	Metacarpal III, right (maximum size). Size Grade I.	Urtyn Obo, 1928.

26388	Metacarpal III, left.	25 miles S. W. of Iren Dabasu, 1930.
26389	Metatarsal III, left.	25 miles S. W. of Iren Dabasu, 1930.
26179	Two calcanea, right and left (unassociated).	Urtyn Obo, 1928.
26174	Calcaneum, left.	Urtyn Obo, 1928.
26189	Patella, astragalus and carpal (no association).	Nom Kong Obo (Holy Mesa), 1928.
18651	Calcaneum and a few fragments of other bones.	Iren Dabasu, 1922.
26190	Atlas vertebra; two calcanea; one metatarsal III, one metacarpal III; three phalanges? (Small size—possibly not *Baluchitherium*.)	Jhama Obo, 1928.

Hsanda Gol Beds
(Tsagan Nor Region)

18650	Skull and fragmentary lower jaws. Type of *Baluchitherium grangeri* Osborn. Size Grade II.	1922.
21618	Fore and hind feet complete except left hind foot which lacks tarsus. Size Grade IV.	1925.
18652	Distal end of humerus, left (found near skull No. 18650).	1922.
20446	Proximal ends of ulna and radius.	1922.
21619	Femur, left; dorsal vertebra (no association). Size Grade IV.	1925.
21749	Proximal end of left metatarsus, and one indet. foot bone.	1925.

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PLATE I

Endocranial cast of *Baluchitherium grangeri*. Type skull.

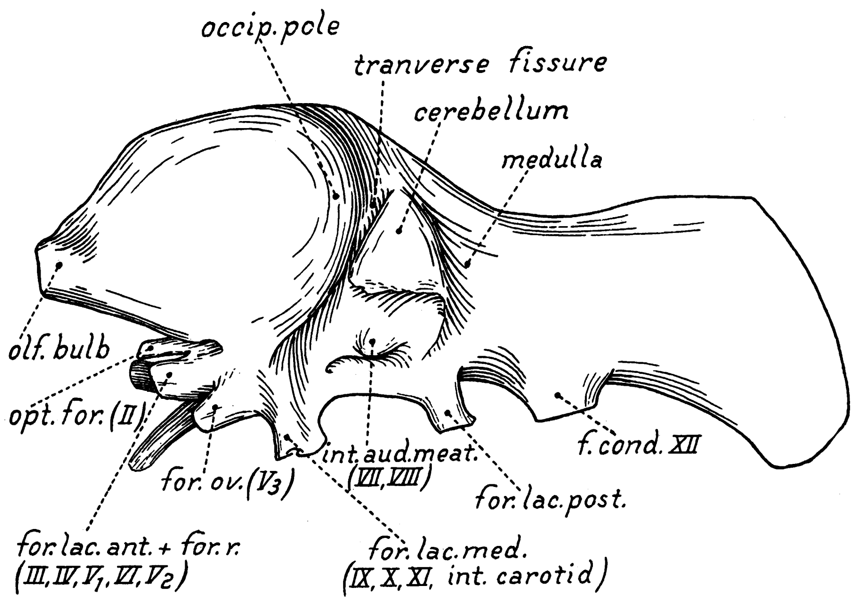
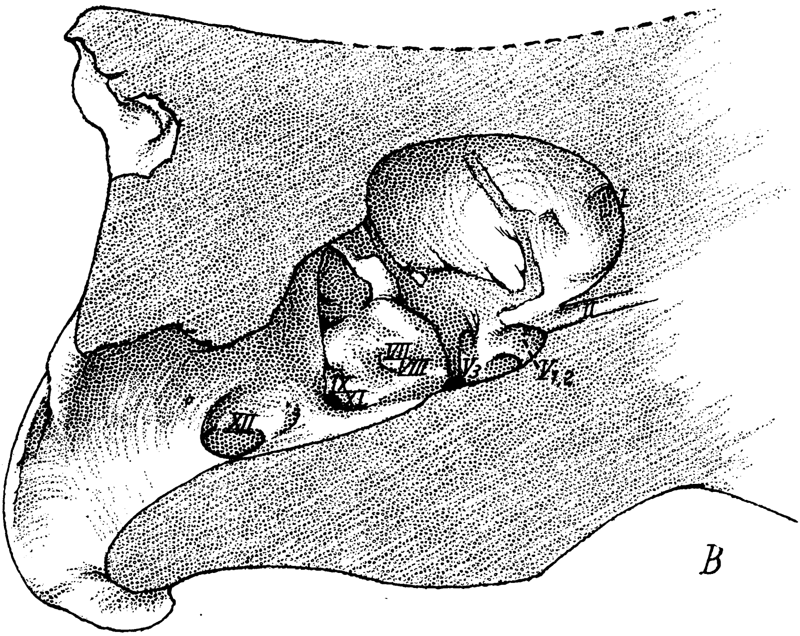
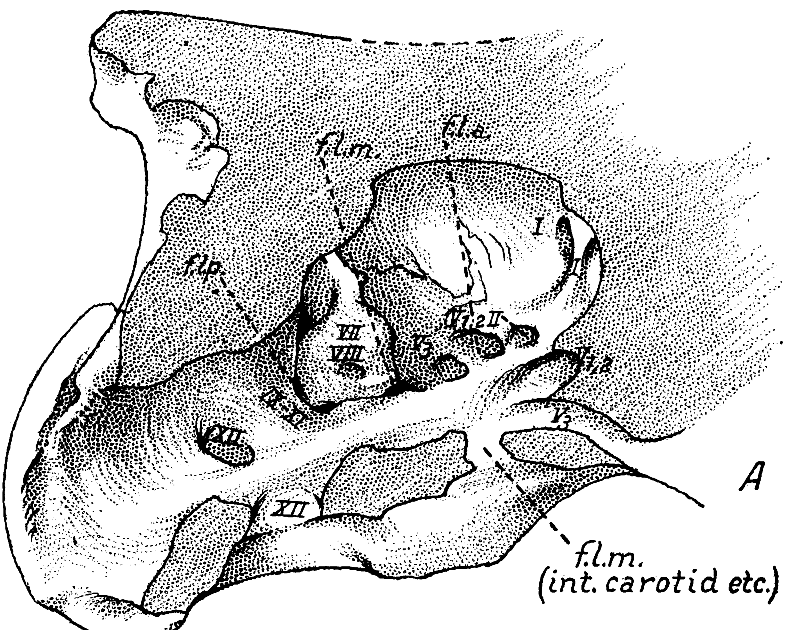

occip. pole
tranverse fissure
cerebellum
medulla
olf. bulb
opt. for. (II)
for. ov. (V3)
int. aud. meat. (VII, VIII)
for. lac. post.
f. cond. XII
for. lac. ant. + for. r. (III, IV, V1, VI, V2)
for. lac. med. (IX, X, XI, int. carotid)

PLATE II

Interior of braincase of *Baluchitherium grangeri*. Type skull. *A*. Oblique view. *B*. Inner side view, partly restored.


VII
VIII
V3
V1,2
II
XII

B


f.l.m.
f.l.a.
f.l.p.
I
VII
VIII
V3
XII
XII
f.l.m.
(int. carotid etc.)

A

Plate III

Sixth cervical vertebra of *Baluchitherium grangeri* compared with that of white rhinoceros (*Ceratotherium simum*). About 1/3 natural size.

PLATE IV

Model of *Baluchitherium grangeri* to scale with six-foot man. By John W. Hope.