

The largest land mammal ever imagined

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The Oligocene giant rhinocerotoid *Indricotherium transouralicum* (= *Baluchitherium grangeri*), ‘the largest mammal that ever lived,’ was smaller than is generally believed. Over 90 estimates based on head-and-body length, skull size, molar length and proximal limb bone diameters agree well on a mean mass estimate of about 11 tonnes (t) rather than the 20–30 t given by most texts. A maximum mass estimate between 15 and 20 t seems probable. Marked sexual dimorphism is possible but the material is insufficient to assess the problem properly. The single source of the inflated, widely cited mass estimates seems to be the famous Granger-Gregory-Ziska reconstruction from 1935–36, which was itself inflated by arbitrary, isometric scaling up of individual elements to a hypothetical maximum size. *Paraceratherium bugtiense* and *P. proborovi* seem to have been somewhat smaller than *I. transouralicum*. The largest indricotheres were similar in size to the largest fossil proboscideans, and extend the known size range of terrestrial mammals marginally if at all.

ADDITIONAL KEY WORDS:—*Baluchitherium* – *Indricotherium* – *Paraceratherium* – giant rhinoceros – body size.

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INTRODUCTION

As every palaeontological textbook testifies, the gigantic Oligocene rhinocerotoid *Indricotherium* (= '*Baluchitherium*') was the largest known land mammal. Exactly how large is a debatable point. Many authors cite 20 tonnes (t) but considerably higher estimates have also been given. Thus Alexander (1989) estimated 34 t, while Savage & Long (1986: 193) suggested a value 'around 30 tonnes', which they said is 'four and a half times as heavy as the heaviest recorded elephant (6.6 tonnes), and nearly twice the estimated weight of the heaviest mammoth'. This quotation reflects the main theoretical significance of *Indricotherium*: if it really was such a giant it would extend the known size range of land mammals considerably, defeating the argument that a mammal necessarily has to remain smaller than a big dinosaur (e.g. Andrews, 1937; Schmidt-Nielsen, 1984; Alexander, 1989).

Following the Mongolian Expeditions of the American Museum of Natural History in the 1920s, the Mongolian Colossus was presented to the public in very definite terms as 'the biggest land mammal that ever lived' (e.g. Andrews 1926, 1928, 1929; Chardin, 1930; Osborn, 1923a; Sowerby, 1929). However, these early reports gave very general and approximate size estimates and did not consider the animal's mass. Although measurements of respectable fossil samples have been available for some time (Granger & Gregory, 1935, 1936; Gromova, 1959), the single foundation of the high mass estimates seems to be the famous and often reproduced reconstruction drawings by Helen Ziska figured by Granger & Gregory (1935: figs 1-2; 1936: figs 46-47; Gregory, 1935).

It seems to have escaped notice that the reconstruction presented by Granger & Gregory was not simply a composite of the fossils at hand, but involved considerable extrapolation based on rather questionable assumptions. Very briefly, Granger & Gregory's method was the following. First the fossils were arbitrarily sorted into four size classes (grades I-IV), assuming the proportions of an 'ordinary' rhinoceros (Granger & Gregory, 1936: 69). The largest class of largest size (grade I) was represented by only three specimens: two cervical vertebrae (AMNH 26168) and one incomplete third metacarpal (AMNH 26175). In order to estimate the sizes of the missing elements in grade I, Granger & Gregory used the better represented smaller grades II-IV. This was done by first estimating the complete size of the incomplete grade I metacarpal, and then calculating size ratios between this and the corresponding metacarpals of the smaller grades. Based on this exercise Granger & Gregory concluded that the third metacarpal of grade I was 1.4 times the linear size of that of grade IV, and indeed that all the skeletal elements could be scaled between the grades, using the coefficients 1, 1.2, 1.3 and 1.4 for grades IV, III, II and I, respectively. The famous reconstruction was thus created by simple isometric scaling up of all elements, save two cervical vertebrae and a metacarpal, by more or less arbitrarily assigned constants. It is thus a highly speculative creation indeed, and mass estimates based on it must be called into question, especially since the scaling of mammalian skeletons is well known to be allometric (e.g. Alexander *et al.*, 1979; Gingerich, 1990; MacMahon, 1973, 1975). In addition, one of the grade IV individuals (AMNH 21618) used for the scaling manipulations is a subadult, introducing an elusive factor of ontogenetic allometry into an already sufficiently messy equation.

Considering the wide general interest in 'the largest land mammal' and its theoretical importance for such central topics as scaling and constraints on body size evolution (e.g. Economos, 1981; Schmidt-Nielsen, 1984), it is quite surprising that palaeontologists have taken so little interest in the much cited size mass estimates. None of the contributors to a recent volume devoted entirely to body size estimation in mammalian palaeobiology (Damuth & MacFadden, 1990) even mention it. An exception is Gingerich (1990), who estimated the body mass of *Indricotherium* from limb bones, using regression equations from a set of living mammals encompassing seven orders (but lacking perissodactyls). Although his results showed a certain degree of scatter, Gingerich concluded that 9 t might be a reasonable estimate for size 'grade II' (the largest size represented by good material), whereas 14 to 15 t or more might be a reasonable estimate for 'grade I'. These low estimates contrast markedly with the 'super-giant' *Indricotherium* generally conceived and are in fair agreement with our own results. The purpose of the present study is to provide a critical re-examination of the Granger-Gregory-Ziska reconstruction, and to produce new mass estimates based directly on the fossil material. We also make use of the more complete material published by Gromova (1959), and of fossil material recently examined by ourselves.

TAXONOMIC NOTE

A certain amount of taxonomic confusion exists about the indricotheres. Although Matthew (1931) pointed out that *Baluchitherium* Osborn, 1923 is a junior synonym of *Paraceratherium* Cooper, 1911, the name *Baluchitherium* remains in common use. The matter is further complicated by the fact that *Indricotherium* Borissiak, 1915 is regarded as a valid genus by most authors, and that Gromova (1959) synonymized *Baluchitherium grangeri* Osborn, 1923 with *Indricotherium transouralicum* Pavlova, 1922. A recent example of the confusion is that Carroll (1987) followed Radinsky (1967) in referring *Indricotherium* to the Hyracodontidae, but also recognized a separate '*Baluchitherium*' which he considered a rhinocerotid. We are not here concerned with systematics, and do not address the question of whether these forms are best regarded as a separate family (Indricotheriidae Borissiak) or as hyracodontids, but we shall refer to them collectively as indricotheres (see Heissig, 1989; Prothero *et al.*, 1986, 1989; Thenius, 1969). We follow the revision of Gromova (1959) in recognizing both *Indricotherium* and *Paraceratherium* as valid genera, and in synonymizing *Baluchitherium grangeri* Osborn, 1923 with *Indricotherium transouralicum* Pavlova, 1922. This paper is restricted to a discussion of size estimates for this species and a limited comparison with two other giant indricotheres, *Paraceratherium bugtiense* (Pilgrim, 1908) and *P. prohorovi* (Borissiak, 1939).

MATERIALS AND METHODS

We studied postcranial material of *Indricotherium transouralicum* from Mongolia in the American Museum of Natural History (New York) and teeth of *Paraceratherium bugtiense* from Baluchistan in the Natural History Museum (London). We also used measurements taken from Granger & Gregory (1936) and Gromova (1959). The ranges given by Gromova were used as such. For teeth measured by ourselves, only the means were used since our observed range

is more than covered by Gromova's. In the postcranial material most dimensions could only be obtained from single specimens, but where appropriate we give the mass estimate for both the mean and range.

Estimation of body mass from skeletal elements was carried out using least squares regression equations derived from various sets of living ungulates (Damuth & MacFadden, 1990). We also used slightly updated versions of the databases used by Fortelius (1985, 1990), and measurements of postcranial bones of living rhinoceroses from Guérin (1980). The percent prediction error (%PE) of the equations used ranges from about 15% to about 50%, and the percent standard error of the estimate (%SEE) from about 30% to over 100%. The %PE indicates, for each case, the percent difference between the actual mass and that predicted by the equation in question. The mean of the %PE values provides a comparative index of that equation's ability to predict body mass accurately, and we shall use it in this paper to rank equations. For further details on %PE and %SEE see Van Valkenburgh (1990) and references cited therein, for values see Appendix 1 and the relevant chapters and appendices in Damuth & MacFadden (1990).

We used the simple approach of estimating masses from many elements, using several equations for each, and calculating mean estimates based on the values obtained. We performed various corrections for estimation bias, but they did not influence the mean estimates significantly (see Discussion). Thus the method either works remarkably well, or else all the fossil evidence gives a uniformly biased estimate. The latter possibility appears unlikely and very difficult to assess. The precision of this method is unknown but it is certainly much greater than that of any single component equation.

The elements and measurements were chosen according to availability, using criteria from Damuth & MacFadden (1990). For limb bones proximal elements are better mass estimators than distal ones, and diameters are better than lengths (Scott, 1990). We thus used all available measurements for humerus and femur, and various diameters for radius and tibia. For molars, lengths are better estimators than widths or areas, at least for ungulates (Fortelius, 1990; Janis, 1990; Damuth, 1990), and we consequently used molar lengths.

RESULTS

Head-and-body length

Two skeletal reconstructions of *Indricotherium transouralicum* are available for estimation of head-and-body length: Granger & Gregory (1935: figs 1–2; 1936: figs 46–47) and Gromova (1959: fig. 25). The latter yields an approximate head-and-body length of 740 cm, assuming that the skeleton is correctly mounted and the scale of 1 : 40 is correct. Andrews (1929) estimated the head-and-body length of '*Baluchitherium*' at 24 ft or about 730 cm, a remarkably similar figure. Using Damuth's (1990) equations a head-and-body length, of 740 cm yields mass estimates of 13.0 t (based on 'all ungulates') and 16.3 t (based on 'non-selenodonts') (Table 1).

As expected from its scaled-up nature discussed in the introduction, the reconstruction by Granger & Gregory (1936: 46–47) gives a much greater head-and-body length, about 870 cm. This yields the mass estimates of 21.5 t and

TABLE 1. Mass estimates for *Indricotherium transouralicum* from head-and-body length

Source	HBL (cm)	Estimate (t) (equations from Damuth, 1990)		
		All ungulates	Non-selenodonts	Mean
Gromova (1959)	740	13.0	16.3	14.7
Granger & Gregory (1936)	870	21.5	27.0	24.3
Grade II*	725	12.1	15.1	13.6
Grade III*	669	9.4	11.8	10.6
Grade IV*	621	7.4	9.3	8.4

*Reduced from Grade I by coefficients used by Granger & Gregory (1936).

27.0 t, again using Damuth's (1990) equations for all ungulates and non-selenodonts, respectively (Table 1). These values correspond well to the previous estimates of 20–30 t based on the same reconstruction.

The effect that Granger & Gregory's manipulations have on mass estimates may be illustrated by reducing the length of the whole reconstruction by their scaling coefficients. Dividing the head-and-body-length of the grade I reconstruction by these coefficients results in a series of mass estimates from 16 to 7 t, with a grand mean for grades II–IV of 11.5 t (Table 1).

Gromova's (1959) reconstruction is also a composite, but unlike Granger & Gregory's, it is based on the sizes and proportions actually found in the fossil material (from the locality Chelkar-Teniz in Kazakhstan). The mount is faulty in several respects, notably in the straight rather than flexed limbs, but the head-and-body length should not be significantly affected by these problems. The two reconstructions are remarkably different in size and proportions. In Gromova's animal the neck and limbs are strongly elongated, recalling earlier reconstructions by Osborn (e.g. 1923a, b). In contrast, Granger & Gregory's beast shows the massive proportions of the 'normal' rhinoceros assumed in the process of scaling all elements to 'grade I'. It can hardly be a coincidence that the two parts that differ most are the neck and the feet, i.e. the parts purportedly represented by fossils of grade I in the Mongolian material. [Granger & Gregory (1936: 19–20) did discuss the unusual, rather horse-like shape of the cervical vertebrae, remarked on already by Cooper (1923), but did not consider the possibility of an elongated neck, concluding instead that the neck was normally held downwards.]

The single, incomplete 'grade I' third metacarpal from Mongolia ('AMNM 26175), with a reconstructed length of about 65 cm, is not far beyond the size range of 51.7–61.5 given by Gromova (1959) [the longest complete Mc III reported by Granger & Gregory (1926) was assigned to grade II and measured only 53.2 cm in length]. Granger & Gregory evidently overlooked the fact that the limbs of *Indricotherium* are elongated, and assumed the metacarpal to be as relatively short as in the average rhinoceros. The rest of the animal was, inevitably, blown up to match this assumption.

There seems every reason to accept that *Indricotherium transouralicum* did indeed have the elongated neck and limbs suggested by the proportions of the material preserved, as did Osborn (1923a, b) and Gromova (1959). If Granger & Gregory's reconstruction is arbitrarily reduced to their grade II (the largest supported by good fossil evidence), it yields mass estimates about 1 t below those

of Gromova's (Table 1). Thus head-and-body length estimates agree robustly on a mass not much above 15 t for the largest individuals of *Indricotherium transouralicum*.

Skull

The only good skull available appears to be the type of *Baluchitherium grangeri* Osborn, described in detail by Granger & Gregory (1936) and assigned by them to grade II. Inserting the values given by Granger & Gregory (1936: table I) into a number of allometric equations from various sources produces estimates in the range 7–16 t (grand mean 9.6 t), with the single high estimate of 19.8 t given for skull length by an equation based on rhinoceroses and the relatively short-skulled hyraxes (Table 2). *Indricotherium* had a very long and relatively narrow skull, which means that mass is probably somewhat overestimated by skull length and underestimated by width. In combination these biases should cancel each other to some extent.

Teeth

Gromova (1959: tables 5, 8) gives comparative molar measurements in the form of ranges for *Paraceratherium bugtiense*, *P. prohorovi* and *Indricotherium transouralicum*. We used these and the original measurements of *Paraceratherium bugtiense*. The mass estimates show a fair scatter but they fall mainly within the brackets of 5–15 t for all three species (Table 3). The molars of *Paraceratherium prohorovi* give the highest mass estimates (grand mean 10.7 t), those of *P. bugtiense* the lowest (grand mean 6.5 t). For *I. transouralicum* the minimum estimates range from 3 to 11 t, the maximum estimates from 5 to 17 t, with a grand mean of 8 t. The molars thus generate somewhat lower mass estimates than head-and-body length or skull size, at least for *I. transouralicum*.

Proximal limb-bones

As with the previous categories, the limb-bones largely agree on estimates in the range 5–15 t, except that the lengths of humerus and femur give occasional values over 20 t for the long-legged *I. transouralicum* (Table 4). Indeed, Granger & Gregory (1936) themselves remarked on the relatively long humeri and femora of this species. Disregarding estimates based on bone length, the range for *I. transouralicum* is from 5 to 17 t. Gromova's (1959) values for the Kazakhstan sample give a somewhat higher grand mean than the Mongolian material measured by us (grand mean 10.6 t vs 8.4 t), but both values lie in the range covered by cranial and dental estimates. For *P. bugtiense* non-length mass estimates range from 9 to 15 t (grand mean 11.7 t), considerably higher than the 6–7 t suggested by dental estimates. The corresponding estimates for *P. prohorovi* lie mainly between 3 and 12 t (grand mean 7.1 t), with two aberrantly high estimates at 17 t. Thus for this species the estimates based on limb bones are much lower than those based on molars (cf. Tables 3, 4).

TABLE 2. Mass estimates for *Indricotherium transouralicum* from skull size

Dimension (Granger & Gregory, 1936) (type of <i>B. grangeri</i>)	Size (cm)	Estimate (t) (equations from Janis, 1990)		Estimate (t) (equations from Fortelius, (unpublished data as in Fortelius, 1985, 1990)			Mean
		All ungulates	Hyraco-periss*	All ungulates	Non-selenodont	Hyraco-rhino*	
Basicondylar length	128.6	8.5**	7.4**	8.9	13.3	19.8	12.1
Zygomatic width	61.4	—	—	8.5	7.3	11.9	7.0
Length x width	7896.0	—	—	10.0	9.8	15.4	9.7
Mean				9.1	10.1	15.7	9.6

*Hyraco-periss = Hyracoidea + Perissodactyla: Hyraco-rhino = Hyracoidea + Rhinocerotidae.

**Probably underestimates, as equations for total skull length were used. Those for basicondylar length give the impossible estimates 358.7 and 175.8, respectively.

TABLE 3. Mass estimates for indricotheres from tooth row and molar lengths

Dimension	N	Size (mm)	Mass estimates (t) based on equations from sources indicated										
			Damuth (1990)			Janis (1990)			Fortelius (unpublished)				
			All ungulates	Non-selenodont	All ungulates	All ungulates	Hyraco-perisso*	All ungulates	Hyraco-rhino*	Rhinoceroses	Mean		
<i>Indricotherium transouralicum</i> , Mongolia (Granger & Gregory, 1936)													
TRLU**	1	403	—	—	—	—	—	6.7	7.2	4.8	6.2		
<i>Indricotherium transouralicum</i> , Chelkar-Teniz, Kazakhstan (Gromova, 1959)													
M1/L	8	66-88	6.8-16.5	5.9-14.4	—	—	—	4.9-11.2	5.1-7.4	—	9.0		
M2/L	5	85-96	8.1-11.6	6.3-9.1	11.2-16.5	8.0-11.4	—	6.7-9.5	6.6-9.6	9.3-14.8	11.6		
M3/L	5	98-111	7.6-10.9	6.7-7.4	—	—	—	5.8-8.1	7.6-11.0	10.8-16.7	9.3		
M1/L	3	60-69	5.9-9.1	4.8-7.4	7.5-11.9	5.5-10.9	—	—	—	—	7.9		
M2/L	6	69-80	5.2-8.2	3.4-5.3	6.5-10.5	5.5-8.6	—	—	—	—	6.6		
M3/L	3	80-92	3.1-4.7	3.1-4.5	4.7-7.4	7.4-11.3	—	—	—	—	5.8		
mean			8.1	6.5	9.5	8.6	—	7.7	7.9	12.9	8.5		
<i>Paraceratherium bugtiense</i> , Dera Bugti, Baluchistan, The Natural History Museum, London (orig. data)													
M1/L	4	68.0	7.5	6.4	—	—	—	5.3	5.7	—	6.2		
M2/L	8	75.5	5.6	4.5	7.7	5.7	—	4.8	4.6	6.0	5.6		
M3/L	8	89.2	5.9	4.2	—	—	—	4.6	6.2	7.7	5.7		
M1/L	1	68.0	8.7	7.1	11.3	8.3	—	—	—	—	8.8		

LARGEST LAND MAMMAL

M/2L	3	72.3	6.0	4.5	13.8	10.0	—	—	—	8.6
M/3L	2	75.5	2.6	2.9	3.9	6.2	—	—	—	3.9
mean			6.0	4.9	9.2	7.6	4.9	5.5	6.8	6.4
<i>Paraceratherium bugtiense</i> (Gromova, 1959)										
M1/L	—	68-80	7.5-12.3	6.4-10.7	—	—	5.3-8.5	5.7-9.5	—	8.2
M2/L	—	74-96	5.3-11.6	4.2-9.1	7.2-12.5	5.4-11.4	4.5-9.5	4.3-9.6	5.5-14.8	8.2
M3/L	—	74-96	3.5-7.2	2.5-5.1	—	—	2.8-5.5	3.3-7.2	4.0-10.0	5.1
M1/L	1	65	7.6	6.1	9.8	7.2	—	—	—	7.7
M2/L	2	75-77	6.7-7.3	5.0-5.4	8.5-9.3	7.1-7.7	—	—	—	7.1
M3/L	2	75-78	2.5-2.8	2.8-3.1	3.9-4.4	2.4-6.9	—	—	—	3.7
mean			6.8	5.5	7.9	6.9	6.0	6.6	6.9	6.7
<i>Paraceratherium prohorovi</i> (Gromova, 1959)										
M1/L	5	73-89	9.3-17.1	8.0-14.9	—	—	6.5-11.6	7.1-13.4	—	11.0
M2/L	4	96-108	11.6-16.6	9.1-12.9	16.5-24.1	11.4-16.1	9.5-13.4	9.6-13.9	14.8-23.1	14.5
M3/L	5	100-117	8.1-12.6	5.6-8.5	—	—	6.2-9.3	8.1-12.8	11.6-20.1	10.3
M1/L	3	67-76	8.3-12.3	6.7-10.1	10.8	7.9-11.8	—	—	—	9.7
M2/L	7	71-83	5.7-9.2	4.2-6.7	7.2-11.8	6.0-9.6	—	—	—	10.1
M3/L	8	80-96	3.1-5.6	3.1-5.6	4.7-8.5	7.4-12.8	—	—	—	6.3
mean			10.0	7.9	11.9	10.4	9.4	10.8	17.4	10.5

*Hyraco-perisso = Hyracoidea + Perissodactyla; Hyraco-rhino = Hyracoidea + Rhinocerotidae.

**Upper toothrow length.

TABLE 4. Mass estimates for indricotheres from limb bones

Dimension [Scott (1990) symbols] Prediction equations for all ungulates from Scott (1990), for rhinoceroses bone measurements from Guérin (1980) and body masses from the literature (Fortelius, 1985)	N	Size (cm)	Estimate (t)		
			All ungulates	Rhinoceroses	Mean
<i>Indricotherium transouralicum</i> (AMNH, original data)					
Humerus length (H2)	1	98.5	18.0	14.7	16.4
Humerus distal width (H5)	1	27.2	9.6	10.8	10.2
Radius proximal width (R4)	1	26.6	6.4	10.3	8.4
Radius proximal a-p diam. (R3)	1	17.1	15.4	12.1	13.8
Radius distal width (R5)	1	24.3	6.8	9.7	8.3
Femur length (F1)* (mean)	4	108.5	15.3	9.8	12.6
(observed range)		(94.0-119.0)	(9.2-21.0)	(7.0-21.1)	
Femur distal width (Granger & Gregory, 1936) (F5)	1	27.1	9.5	5.8	7.7
Tibia proximal width (T2)	1	28.3	8.9	16.0	12.5
Tibia distal width (T4)	1	16.5	4.0	5.7	4.9
Tibia distal a-p diam. (T5)	1	13.2	7.7	5.8	6.8
Mean			10.2	10.1	10.1
<i>Indricotherium transouralicum</i> (Gromova, 1959)					
Humerus length (H2)	1	93.2	14.9	12.7	13.8
Humerus caput width (H3)	1	24.2	10.4	—	10.4
Humerus distal width (H5)	1	31.2	13.6	14.3	13.95
Radius proximal width (R4)	1	24.1	5.0	8.4	6.7
Radius distal width (R5)	1	31.8	13.0	17.2	15.1
Femur length (F1)*	1	123.0	23.6	13.0	18.3
Femur distal width (F5)	1	27.0	9.4	5.7	7.6
Tibia proximal width (T2)	1	28.0	7.5	15.5	11.5
Tibia distal width (T4)	2	18.8-21.2	5.6-7.6	7.0-8.4	7.2
Tibia distal a-p diam. (T5)	2	15.8-17.0	12.9-16.0	8.7-10.3	12.0
Mean			11.9	11.6	11.8
<i>Paraceratherium bugtiense</i> (Gromova, 1959)					
Humerus length (H2)	—	84.8	10.8	9.9	10.4
Humerus caput width (H3)	—	23.8	9.9	—	9.9
Humerus distal width (H5)	—	31.8	14.3	14.9	14.6
Femur length (F1)*	—	120.0	21.7	12.2	17.0
Tibia distal width (T4)	—	23.0	9.4	9.6	9.5
Mean			13.2	11.7	12.4
<i>Paraceratherium prohorovi</i> (Gromova, 1959)					
Humerus length (H2)	1	62.3	3.8	4.4	4.1
Humerus caput width (H3)	1	20.0	6.2	—	6.2
Humerus distal width (H5)	5	21.9-27.0	5.5-9.4	6.8-10.6	8.1
Radius proximal width (R4)	8	18.0-34.2	2.5-11.6	4.5-17.4	9.9
Radius distal width (R5)	1	22.8	5.8	8.4	7.1
Femur distal width (F5)	1	20.0	4.1	3.1	3.6
Tibia proximal width (T2)	2	19.3-28.9	2.6-8.2	5.2-17.0	8.3
Tibia distal width (T4)	5	14.3-18.5	2.7-5.4	4.5-6.8	5.7
Tibia distal a-p diam. (T5)	3	12.0-15.2	5.8-11.6	4.7-8.0	7.4
Mean			5.8	7.7	6.7

*Scott's F1 (joint-to-joint length) was used, as her equation for total length (F2) gives unreasonable estimates around 200 t instead of lower than for F1 as it should. The estimates shown are presumably too high.

DISCUSSION

As pointed out by Damuth (1990), the range of mass estimates reflects several factors which can be subsumed under the headings of imprecision and bias. In

TABLE 5. Mean mass estimates for *Indricotherium transouralicum* based on subsets of the estimates from Tables 1-4

Subset	Mean	N	CV
All estimates*	10.1	92	38
'Worst' predictors** eliminated	9.5	79	35
Only 'best' predictors*** included	11.1	27	31
Estimates outside the raw mean ± 1 s.d.	9.5	64	23
Equations with % PE > 50 eliminated	10.2	89	37
Equations with % PE > 40 eliminated	10.6	77	36
Equations with % PE > 30 eliminated	10.9	54	38
Equations with % PE > 20 eliminated	10.8	17	37

*Excluding the obviously inflated head-and-body length of Granger & Gregory's grade I reconstruction.

**Limb bone lengths, skull length-based mass estimates based on Janis (1990) and our equation for hyracoids and rhinoceroses, the Granger & Gregory hand-and-body length scaled to grade IV.

***Head-and-body length of Gromova, head-and-body length of Granger & Gregory scaled to grade II, all diameters of humerus and femur, proximal diameters of radius and tibia.

the present case both may be expected to have an unusually great influence, as the size of giant indricotheres lies beyond that of any available living reference group. However, although the individual estimates are uncertain they are based on a variety of elements representing different functional complexes. This means that biases should in principle be independent between, for example, teeth and limb bones. This is supported by the consistent patterns seen, such as the low estimates based on molars, except for *P. prohorovi* which has highly reduced premolars and correspondingly enlarged molars (Gromova, 1959), resulting in anomalously high molar-based estimates. The use of different reference sets also allows a certain degree of control of bias. For example, an equation based on hyraxes and rhinoceroses gives a high mass estimate based on skull length, as expected since hyraxes have relatively short skulls.

The problem here is not so much to quantify the uncertainty of individual estimates but rather to extract some reasonable combined mass estimate. The simplest combination is simply the mean of all estimates (using midpoints when only ranges are known). A somewhat better estimate is obtained if values that can be expected to be biased are eliminated (estimates based on limb bone lengths, or obtained using equations that include a known bias: see Tables 2, 4). A possibly better but also more questionable estimate can be calculated by using only those dimensions believed for various reasons to be the most reliable predictors (see Table 5). As a more neutral alternative one might use the mean of all estimates that lie within one standard deviation of the raw mean. Finally, one might use some statistical parameter such as the percent prediction error (%PE), eliminating estimates produced by equations associated with high error values. Performing these manipulations for *I. transouralicum* shows, however, that they have very little effect (Table 5). The raw mean of all estimates (excluding the obviously inflated head-and-body length of Granger & Gregory's grade I reconstruction) is 10.1 t, eliminating the 'worst' predictors decreases the value to 9.5 t, while using only the 'best' predictors increases it to 11.1 t. Removing values outside ± 1 s.d. of the raw mean gives the value 9.5 t. When the few equations with %PE values above 50 are eliminated, the mean estimate is 10.2 t.

Removing equations with %PE values over 40 gives 10.6 t, while removing those with %PE over 30 gives 10.9 t, a value almost identical to the 10.8 t given by the 17 estimates with %PE of 20 or less. In each case the median is slightly lower, but always within about 1 t of the mean. The coefficient of variation is quite insensitive to these operations, staying in the range 30–40 except when the standard deviation itself is used as a criterion for pruning (Table 5). The data thus agree robustly on a value around 10 t, with the best predictors converging remarkably on a mean about 11 t. Certainly a precision finer than whole tonnes is unrealistic given the multitude of unknowns compounded by extrapolation well beyond the size range covered by the reference data. We conclude that a mean size of 11 t (plus or minus a few tonnes) is the best estimate obtainable for this species.

Damuth (1990) concluded that the best estimator of ungulate body mass was a multiple regression equation that includes head-and-body length and lower molar length. On the suggestion of Dr Damuth (personal communication, 1991) we approximated the latter measure by summing the smallest and the largest individual lower molar lengths, respectively. This yielded an estimated lower molar row length range of 209–241 mm. With a head-and-body length of 7400 mm Damuth's equation gives a corresponding mass range of 11.1–12.4 t, in good agreement with the 11 ± 1 few tonnes suggested by the estimates discussed above.

Estimating mean mass ignores the problem of size range and, especially, the perpetual problem of sexual dimorphism in fossil organisms. The data at hand are not particularly suitable for investigation of these problems, as they consist of small materials of mainly isolated elements, mostly described only in terms of observed range of variation. The frequency distribution of mass estimates for *I. transouralicum* appears somewhat bimodal (Fig. 1). The bimodality is equally evident for estimates based on the skull, the limb bones, and even the molars, and does not reflect anatomical differences. In each case the lower peak is well below 10 t and the upper around 13 t. For all the 92 estimates pooled, the lower peak is about 7–9 t and the higher peak 13–15 t. The distribution as a whole is skewed to the right, with low estimates more numerous than high estimates.

The sample size for *I. transouralicum* is small enough that the bimodality might represent sexual dimorphism, with some elements representing only males, others only females, and with one sex nearly twice as heavy as the other. Grade I of Granger & Gregory (1936) having turned out to lack empirical foundation, grades II, III and IV might fit such a scheme. Grade IV at 8 t might represent females, grade II at 14 t males and grade III at 11 t a mixture of both (Table 1). Alternatively and quite possibly the frequency distribution of the estimates may be an artifact of the equations used, or simply a small sample effect—estimates for the other species analysed here do not appear bimodal. Any size dimorphism in *I. transouralicum* is unlikely to reflect geological age since it is seen both in the Mongolian material and in the single-locality sample from Chelkar Teniz.

The other species considered here appear to have been somewhat smaller than *Indricotherium transouralicum*. The raw mean estimate for *P. bugtiense* is 7.4 t ($N = 65$), for *P. prohorovi* 9.1 t ($N = 45$). The latter estimate is evidently inflated by the enlarged molars seen in *P. prohorovi*; limb bones suggest only 6.7 t ($N = 17$).

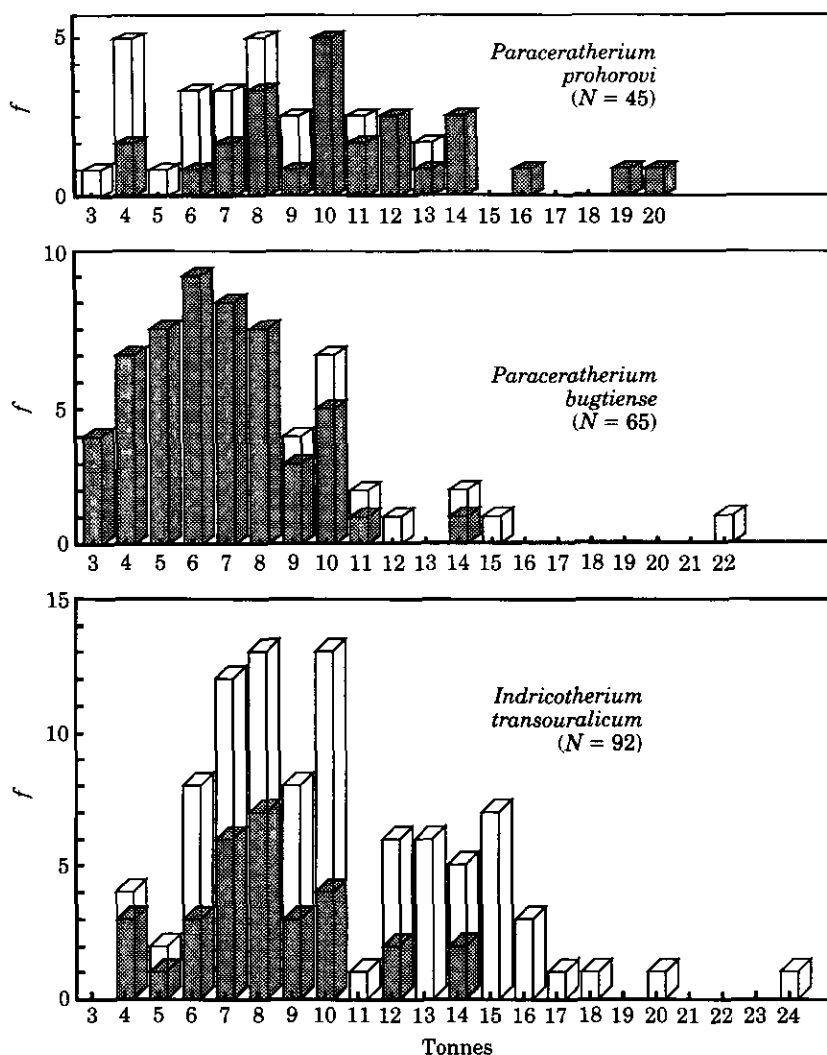


Figure 1. Frequency distributions of mass estimates for the three species of indricothere discussed in the text. Estimates based on molar lengths are shown stippled.

A size range of 15–20 t for the largest indricothere individuals appears similar to that found for the largest fossil proboscideans. The largest individual known may be the mammoth represented by a single humerus from Mosbach. Osborn (1942: 1605) estimated the shoulder height in the flesh of this animal at about 450 cm, while Garutt & Nikolskaya (1988) give the even higher estimate of 500 cm. The largest complete skeleton seems to be a male *Mammuthus trogontherii* from Azov, briefly described and figured by Garutt & Nikolskaya (1988). This individual has a skeletal shoulder height of 450 cm, suggesting a shoulder height in the flesh of about 470–475 cm.

For the estimate of 470 cm shoulder height, the equations tabulated by Roth (1990: table 9.2) produce mass estimates ranging from 13.6 t (based on wild female *Loxodonta*) to 30.7 t (based on captive and wild *Elephas*). Equations based

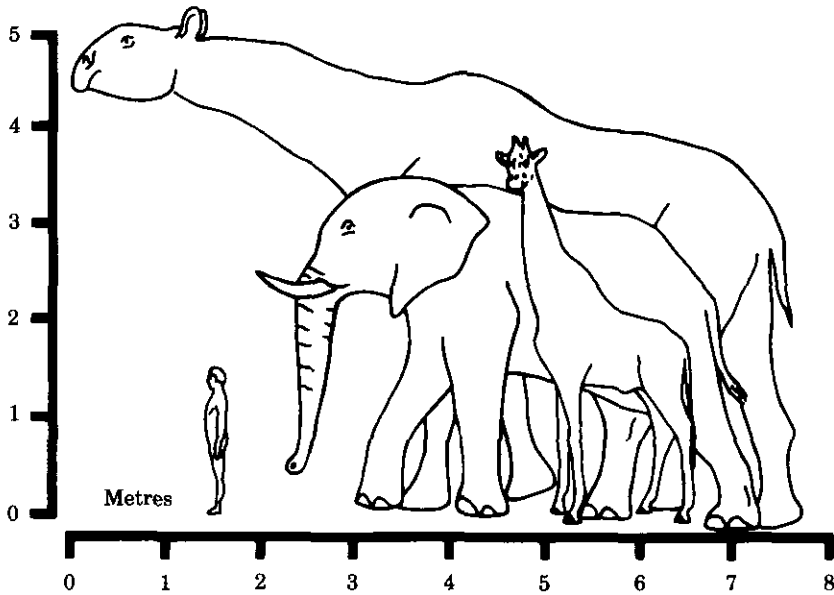


Figure 2. *Indricotherium transouralicum* drawn to scale with a large African elephant bull, a giraffe and a male human. Compiled and modified from several sources (mainly Augusta & Burian, 1956; Bosman & Hall-Martin, 1986; Gregory, 1935).

on populations of wild male *Loxodonta* range from 15.6 to 16.1 t, and the mean of all eight estimates based on populations of *Loxodonta* is 15.8 t. The four estimates based on populations of *Elephas* give a much higher mean of 26.1 t. This contrast probably reflects the simple bias of comparing the relatively low-shouldered *Elephas* with the relatively higher-shouldered *Mammuthus*. The estimates based on high-shouldered *Loxodonta* are probably more realistic, although they, too, may be somewhat high. As for the indricotheres, all these estimates are, of course, uncertain because of extrapolation far beyond the known range.

For comparison it should be noted that the mean of *Loxodonta*-based estimates for a 500 cm shoulder height is 18.9 t, for 450 cm 14.0 t, and even for a 'small' mammoth of 410 cm shoulder height this value is as high as 10.7 t. Based on these data, it would be difficult to argue convincingly that the largest indricotheres were larger than the largest proboscideans—both seem to have been slightly more than twice as heavy as the largest African elephants, the heaviest living land mammals (Fig. 2). Indricotheres thus seem to extend the empirically 'known' size range of mammals marginally, if at all. Certainly they were not twice the size of the largest mammoths.

On the basis of gravitational tolerance of living mammals, Economos (1981) suggested that 20 t might be an approximate upper size limit for land mammals and suggested that '*Baluchitherium*' was close to this limit. Our empirical data do not contradict this, and the possibility remains that mammals, for some presently unknown reason, must remain decidedly smaller than sauropods. But the reason, if it exists, may be ecological rather than biomechanical, possibly related to the markedly different reproductive strategies of mammals and archosaurs (Janis & Carrano, 1992).

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APPENDIX I

Previously unpublished equations used for estimation of body mass in this paper. All other equations used are conveniently tabulated in Damuth & MacFadden (1990). Dimensions in g and mm

Group	Dimension	Slope	Intercept	r^2	% SEE	% PE	N
All ungulates	CBL	3.10	-2.69	0.96	48	31	46
	WZYG	3.03	-1.52	0.93	69	42	46
	CBL X WZYG	1.57	-2.26	0.97	42	27	46
	TRLU	2.99	-0.96	0.93	67	46	44
	M ¹ L	2.89	1.43	0.93	71	50	42
	M ² L	2.89	1.26	0.93	71	48	42
	M ³ L	2.66	1.49	0.86	114	61	41
Non-selenodonts	CBL	3.33	-3.23	0.98	39	27	17
	WZYG	3.23	-2.14	0.96	67	41	17
	CBL X WZYG	1.65	-2.73	0.98	46	31	17
Hyracoidea + Rhinocerotidae	CBL	3.40	-6.28	1.00	68	18	9
	WZYG	3.47	-5.60	0.99	101	23	9
	CBL X WZYG	1.72	-5.94	0.99	75	20	9
	TRLU	3.28	-4.68	0.99	90	20	9
	M ¹ L	3.19	-2.10	0.98	193	26	9
	M ² L	3.09	-2.14	0.99	95	20	9
	M ³ L	2.94	-1.98	0.99	117	21	9
Rhinocerotidae	CBL	3.02	-5.21	0.89	52	13	5
	WZYG	2.68	-3.60	0.40	165	29	5
	CBL X WZYG	1.60	-5.30	0.71	98	20	5
	TRLU	2.41	-2.60	0.50	142	24	5
	M ² L	3.78	-3.33	0.72	94	17	5
	M ³ L	3.50	-2.98	0.93	39	13	5
	H2*	2.65	-3.76	0.23	61	36	5
	H5*	2.09	-1.06	0.53	45	26	5
	R4*	2.09	-1.06	0.53	46	26	5
	R3*	2.17	-0.78	0.44	51	30	5
	R5*	2.14	-1.11	0.54	45	25	5
	F1*	2.29	-2.97	0.26	60	36	5
	F5*	2.08	-1.31	0.25	60	34	5
	T2*	2.95	-3.03	0.37	54	31	5
	T4*	1.57	-0.01	0.16	65	40	5
T5*	2.27	-1.06	0.45	50	28	5	

*Symbols as in Scott (1990), see Table 4. Abbreviations: CBL = basicondylar length, WZYG = zygomatic width, TRLU = upper tooththrow length.