

Palaeogravity calculations based on weight and mass estimates of *Paraceratherium transouralicum*

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Abstract

There is great interest in calculating accurate values for Earth's palaeogravity. One fundamental technique to quantify palaeogravity is to compute weight against mass estimates of ancient animals. This technique is applied to three specimens of the giant prehistoric mammal *Paraceratherium transouralicum*. The results indicate tentative palaeogravities of 0.73g, 0.81g and 0.85g ± 20% at approximately 29 million years ago.

Key words: Palaeogravity, *Paraceratherium transouralicum*

1. Introduction to palaeogravity

A more extensive introduction to the study of palaeogravity was given in Hurrell (2018). The key points identified in that publication were:

- There has been great interest in calculating palaeogravity with a number of authors speculating that ancient life might indicate palaeogravity was less than the present average of 1g (9.81 m/s²).¹
- The weight-mass method was identified as one of the most accurate ways to calculate palaeogravity from ancient life. It can be calculated from:

$$g_a = w_a / m$$

where g_a is palaeogravity at some predefined age, w_a is the weight at that age and m is the mass. Since mass never varies it does not need a subscript to denote its age.

- Accurate values of weight and mass are required to apply this technique. Weight can be determined from the strength of leg bones, and mass can be determined from model reconstructions and tissue density.

Although previous uses of the weight-mass technique have concentrated on dinosaur specimens the results will be just as valid for mammals.

This study of palaeogravity used three specimens of the gigantic mammal *Paraceratherium transouralicum* to calculate palaeogravity.

¹ See for example: Harlé (1911), Kort (1947), Pennycuick (1992, 2008, 2016), Hurrell (1994, 2011, 2012, 2014a, 2014b, 2018, 2019a, 2019b, 2019c, 2019d, 2019e, 2019f, 2019g), Carey (2000), Amirmardfar (2000, 2012, 2016), Erickson (2001), Sato *et al.* (2009), Scalera (2003a, 2003b), Strutinski (2012, 2016a, 2016b), and Maxlow (2014).

2. *Paraceratherium transouralicum*

Early fossil remains of a huge mammal were collected by British, Russia and United States palaeontologists during the first few decades of the twentieth century. Initially the different centres of scientific expertise alternatively named their creatures *Paraceratherium*, *Baluchitherium* or *Indricotherium*. Manias (2015) provides a good description of the early discovery of the fragmentary remains of this huge prehistoric ungulate unearthed by scientific expeditions sent to India, Turkestan and Mongolia. While it was obvious that these fossils were from an immensely large creature the fragmentary nature of the bones made it difficult to determine its exact nature. At first it wasn't even certain they were all from the same creature.

The first finds began at the beginning of the twentieth century with Clive Forster-Cooper, a British palaeontologist and Director of the Cambridge University Museum of Zoology and Natural History Museum in London. During a 1911 expedition to Baluchistan Foster-Cooper found fossils "remarkable for their unusually large size." Perhaps even more remarkably these fossils didn't belong to dinosaurs but an extremely large mammal. Forster-Cooper decided the fossils were so unique they should be defined as a new genus and species, *Paraceratherium huqiiense*. The next year he found more fossil remains consisting of "three other cervical vertebrae, a femur, tibia, part of an ulna, two humeri, and several foot-bones." It was still difficult to determine what type of animal this was but Foster-Cooper (1913) began to suspect that the fragments were "more comparable with those of the Rhinoceros than anything else, in spite of great differences in proportion and size."

British and Russian palaeontologists continued to report the discovery of fossil remains of a giant mam-

mal. These reports attracted the attention of American palaeontologists and in the 1920s the New York's American Museum of Natural History (AMNH) sent a large team to recover fossils from Central Asia. This is regarded as possibly the largest natural science expedition of the early-twentieth century. It consisted of a team of 15-20 American specialists from all branches of scientific knowledge, supported by local assistants. They soon began to find numerous fossils, including some of a colossal mammal.

The exciting discoveries were thought to be a completely new species that was soon named "*Baluchitherium grangeri*" in 1922. The new discovery was heavily publicised in order to recover some of the cost of the expedition, with extensive reports appearing in the daily and periodical press.

The reconstructions involved the whole scientific team at the AMNH which were later followed up with reports in the scientific literature. Early reconstructions illustrated the beast as a large rhinoceros but later reconstructions showed a fairly gracile, long necked animal that probably browsed on the lofty branches of trees. A painting of the living animal browsing on a tree was produced by the artist Charles R. Knight. There is still some doubt today about the length of the animal's neck since a complete fossil of the neck has never been recovered. Indeed, Witton (2016) discusses the various reconstructions of this animal and notes that "...their neck proportions, overall robustness, the development of a proboscis or trunk, and - most recently - the size of the ears are all inconsistent."

The scientists at the AMNH compared their finds with the British and Russian fossils to produce the most realistic model possible. The British had complete legs bones and vertebrae, the Russians had the largest collection but they were not well preserved. Granger & Gregory (1936) published a scientific

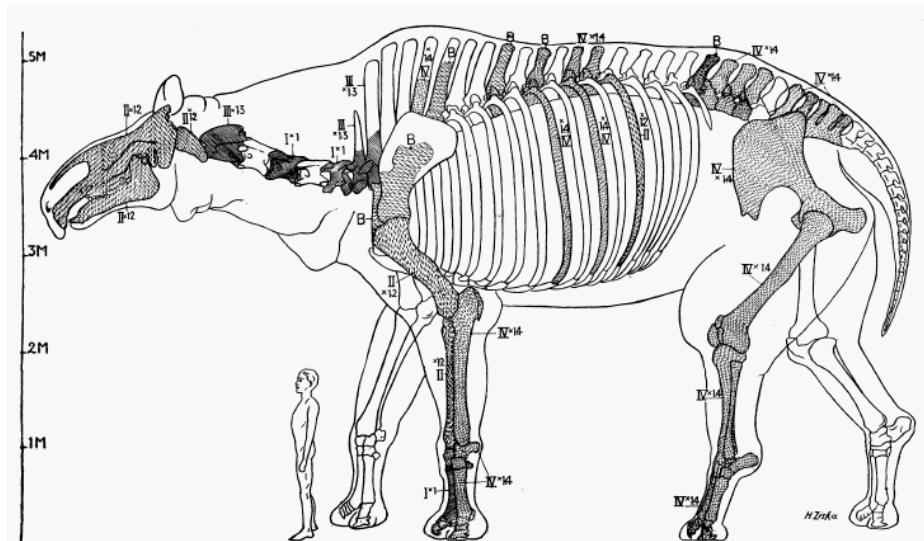


Figure 1. The *Baluchitherium* (*Paraceratherium*) restoration provided in Granger & Gregory (1936, Fig. 46). The differential shading indicates the parts belonging to animals of the four grade of sizes studied by the team - Grade I being the maximum and Grade IV the minimum size. Bones marked B are from the Borissiak collection. See text for further discussion.

paper that managed to encompasses all the different sizes of fossils so far discovered into different sized animals. A Grade I animal was the largest and agreed with some of the largest size estimates that had been given to the popular press. An enormous concrete relief of the Grade I “*Baluchitherium granger*” was erected in the AMNH in 1936, confirming its statistic as “the largest mammal to ever walk the Earth”. The Grade II animal was slightly smaller based on better fossil evidence, while the even smaller Grade IV animal had the most extensive fossil remains but was only half the mass of the Grade I animal. Later palaeontologists would regard the largest Grade I animal as highly problematic, since its enormous size was based on only a few bones.

By the end of the 1930s the largest palaeontological museums in the USA and the Soviet Union both had reconstructions of an enormous prehistoric quadruped. The Americans called their creature *Baluchitherium* while the Russians named their fossil animal *Indricotherium*. Both creatures were described as a gigantic hornless rhinoceros from the Oligocene and Miocene of Central Asia. Both looked similar in appearance although the American reconstruction was noticeably more robustly built than the Russian version.

Despite the different names it was realized that they might all be the same animal. The skull of the Russian exhibit was even a wooden copy of a *Baluchitherium*, sent from America as a gift in the early 1920s, and the American reconstruction was based on extensive comparisons with collects held in Russia and Britain. Size differences between the specimens proved puzzling. In the 1920s, the British palaeontologist Forster-Cooper wrote privately to William Diller Matthew, Curator of Vertebrate Palaeontology at New York’s American Museum of Natural History (AMNH), asking whether sexual dimorphism within the same species could account for the size difference.

Meanwhile the Russian reconstructions tended to produce an animal that was smaller and more lightly built than the American version. Unfortunately the political situation meant that these reconstructions did not seem to be widely known outside of the USSR, with the few foreign visitors in the late 1940s and 1950s commenting that it came as a complete surprise. In the period after the Second World War more specimens were described although they still used differing names.

Today it is generally acknowledged that many of the fossil remains of *Paraceratherium*, *Baluchitherium* and *Indricotherium* were probably from the same species of animal. Since Foster-Cooper was the first to describe

the fossils they took the first name he used, *Paraceratherium*. Despite this they are also still commonly known as *Indricotherium* or *Baluchitherium*.

Even with the fragmentary remains of *Paraceratherium* a great deal has been written about these beasts. Prothero (2013) wrote a whole book about these giant mammals. The painting on the cover of the book suggests a *Paraceratherium* with some additional features. Perhaps they also had a small trunk, or more controversially, large ears.

The taxonomy and systematic nomenclature of these giant *Paraceratherium* have been a matter of ongoing discussion. While it is widely appreciated that several giant *Paraceratherium* species from roughly contemporaneous Oligocene Asian sediments can be identified it is still unclear how many species they represent and how they are related to each other. Even today articles or papers discussing *Paraceratherium* usually require an aside on their confused taxonomy with different authors forming different conclusions. Fortunately the exact taxonomy is not required to calculate palaeogravity. The only requirement is the ability to estimate the mass and weight of particular specimens.

The remarkable size of these mammals has continued to puzzle palaeontologists. How could they grow so large? Just as puzzling was the fact that although they were larger than present day mammals they never attained the size of the largest dinosaurs. As Fortelius & Kappelman (1993) put it, “the possibility remains that mammals, for some presently unknown reason, must remain decidedly smaller than sauropods.” Why were they positioned midway in size between the gigantic dinosaurs and our present-day mammals? The dinosaurs’ large size has produced a range of *ad hoc* theories for their large size but many of these cannot be applied to mammals. In contrast to these *ad hoc* theories, the theory that palaeogravity might have been less still provides an explanation for giant mammals since all life would naturally be shifted towards a larger size in a reduced gravity. Thus palaeogravity during the *Paraceratherium*’s time should in theory have been somewhere between the dinosaurs’ palaeogravity and our present gravity based on their size alone, as explained in Hurrell (2011, 2012) for example. We can check this observation using the weight-mass technique to calculate relatively accurate estimates of palaeogravity when these animals lived.

Paraceratherium lived in Eurasia during the Oligocene period (23 to 34 million years ago) so the age of 29 million years has been used for palaeogravity calculations.

3. Mass estimates from body volumes

The mass of any fossil animal can be estimated by reconstructing a model and using the calculated volume and tissue density to work out the mass of the living animal. However, as the well-known palaeontologist Paul (1988, p134) explained: "Estimating the mass of a fossil species is not an exact science." He considered that the margin of error of an accurately restored model was probably about $\pm 15\%$ even when the skeletal restoration was not missing any major sections. Certainly most estimates fall within this range with only a few outliers.

For the purposes of this palaeogravity calculation we need to specify an optimal mass estimate, or a "best guess", for the specimen. A key aspect of picking an optimal mass estimate from the range of possible options is to understand why mass estimates vary. These are the key factors to consider:

- Unfortunately there is still a great deal of confusion between weight and mass and this has resulted in some palaeontologists trying to produce low mass estimates to conform to weight. Paul (1988, p130) for example explains how he used weight calculated from bone dimensions "to expose implausibly high mass estimates ... so a higher mass estimate should be examined critically." All this general confusion between weight and mass has undoubtedly reduced many mass estimates to unreasonably low values.
- Conway *et al* (2013) have recently criticised "shrink-wrapped" reconstructions, arguing that many of these skinny reconstructions cannot be accurate. They note that while palaeontological artists have been keen to portray most dinosaurs as slim, sleek animals where every muscle can clearly be seen, no living mammal, reptile or bird has such "visible" anatomy. They argue that the use of modern "high-fidelity" musculoskeletal reconstructions indicates that these skinny "shrink-wrapped" reconstructions have gone too far. To illustrate just how unlikely some of these reconstructions are they used the same "shrink-wrapping" method on modern-day animals to produce virtually unrecognisable skinny versions of modern animals.
- Some palaeontologists have decided to completely ignore weight estimates from bone dimensions. The differences between weight and mass estimates are so great for large bipeds that Hutchinson *et al* (2007) concluded that: "...it is almost certain that these scaling equations greatly underestimate dinosaur body masses... Hence, we recommend abandon-

ment of their usage for large dinosaurs." This would indicate that the mass estimates of palaeontologists following this line of reasoning will not be influenced by the general confusion between weight and mass.

It is therefore expected that mass estimates that use "shrink-wrapped" reconstructions will be in the lowest range possible, providing a very useful indication of the minimum mass possible, but probably lower than reality. Palaeontologists who have decided to disregard weight estimates from bone dimensions will be more likely to provide the best mass estimates.

Since *Paraceratherium* was a mammal it should have a density similar to today's mammals. Life today has an average tissue density of about 0.97 tonne cu.m⁻¹. This average value includes the lung volume, typically between 5 to 6 % of body mass for a range of life from small to large. It would seem that an average tissue density of about 0.97 tonne cu.m⁻¹ is a reasonable estimate for *Paraceratherium*.

The first good reconstruction of *Paraceratherium* appeared in the 1930s. The exact size of these creatures was still a matter of debate so the reconstructions presented different-sized versions of the same animal, a Grade I (the largest) down to a Grade IV (the smallest). As Granger & Gregory (1936) explain:

"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. Estimated length (Grade I) in standing pose, from tip of 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." [Granger & Gregory (1936), p65 & 69]

The shoulder heights of the various reconstructions in metric are: Grade I is 5.26 m, Grade II is 4.27 m and Grade IV is 3.66 m. The Grade III reconstruction seems to be used for fossils that didn't fit within the other grades. The Grade I reconstruction has been considered unreliable by a number of palaeontologists because it is based on poorly known fossils, while the Grade II and the Grade IV reconstructions seem to be generally accepted as more reliable. The Grade II animal may be a large male bull *Paraceratherium* while the smaller Grade IV animal is a female.

Gromova (1959) completed a restoration of a Russian specimen to produce a more gracile animal.

Instead of looking like the gigantic buffalo of the American reconstruction this Russian reconstruction looked more like a gigantic giraffe-shaped animal.

Alexander (1989, p161) used the American reconstruction to estimate the mass of the largest Grade I *Paraceratherium*. Since the reconstruction showed an animal that was roughly buffalo-shaped, he scaled up a 0.75 tonne African buffalo to calculate the mass. The head and tail of *Paraceratherium* (excluding the tail) are 9.2 metres long. The same measurement for the buffalo is 2.6 metres. The mass of the largest specimen of *Paraceratherium* would be $0.75 \times (9.2/2.6)^3 = 33.2$ tonnes (Alexander rounds this up to 34 tonnes). This would mean that the Grade II animal would be $33.2 \times (14/17.25)^3 = 17.7$ tonne, and the Grade IV animal would be $33.2 \times (12/17.25)^3 = 11.2$ tonne.

Fortelius & Kappelman (1993, p90) advocate,

"a size range of 15-20 t for the largest indricotheria individuals. ... The head and body length estimates agree robustly on a mass estimate of not much above 15 t for the largest individual of *In. trans.*"

Paul (1997) produced a new skeletal reconstruction and used that to produce a mass estimate. As he explained, he first started with the reconstruction of Granger & Gregory (1936):



Figure 2. The commercially available *Paraceratherium* model produced by CollectA. Note how this reconstruction is generally lighter than the rhinoceros-like iterations of the 1930s as seen in Figure 1. See text for further discussion.

Table 1.

Mass and weight estimates in tonne for one large and two small specimens of *Paraceratherium transouralicum*. See text for further discussion.

Mass and weight estimates in tonnes for <i>Paraceratherium transouralicum</i> (AMNH No 26166 Grade II)				
Mass from models tonne				
Reference	Mass	Notes	Density tonne/cu.m	Volume cu.m
Alexander (1989)	34.00	Based on Grade I animal with buffalo body plan.	1.00	34.00
This paper	23.20	Alexander (1989) with corrected size	1.00	23.20
Gingerich (1990)	14.50	Between 14-15 tonne for the largest specimen.		
Fortelius & Kappelman (1993)	17.50	Between 15-20. From head & body length - no model.		
Paul (1997)	16.40	"biggest bulls" from skeletal reconstruction.	0.96	17.08
Prothero (2013)	17.50	Between 15-20 tonne more realistic.		
Larramendi (2015)	17.40	GDI method based Paul (1997).		
Model	17.27	Scaled to size estimate by Paul (1997)	0.97	17.81
Best estimate	17.00		0.97	17.53

Weight from leg stress tonne(f)				
Reference	Weight	Notes		
Bone dimension	12.48	Quadrupedal calculation		
Best estimate	12.48			

Within ± 20%
 Best gravity estimate **0.73**
 Average Age 29

Mass and weight estimates in tonnes for <i>Paraceratherium transouralicum</i> (AMNH Grade IVa)				
Mass from models tonne				
Reference	Mass	Notes	Density tonne/cu.m	Volume cu.m
This paper	11.20	Alexander (1989) with corrected size		
Gingerich (1990)	9.00	Based on Grade II bone lengths - no model.		
Model	10.00	Scaled to Paul (1997) size estimate	0.97	10.30
Best estimate	10.50		0.97	10.82

Weight from leg stress tonne(f)				
Reference	Weight	Notes		
Bone dimension	8.51	Quadrupedal calculation		
Best estimate	8.51			

Within ± 20%
 Best gravity estimate **0.81**
 Average Age 29

Mass and weight estimates in tonnes for <i>Paraceratherium transouralicum</i> (AMNH Grade IVb)				
Mass from models tonne				
Reference	Mass	Notes	Density tonne/cu.m	Volume cu.m
This paper	11.20	Alexander (1989) with corrected size		
Gingerich (1990)	9.00	Based on Grade II bone lengths - no model.		
Model	10.00	Scaled to Paul (1997) size estimate	0.97	10.30
Best estimate	10.50		0.97	10.82

Weight from leg stress tonne(f)				
Reference	Weight	Notes		
Bone dimension	8.92	Quadrupedal calculation		
Best estimate	8.92			

Within ± 20%
 Best gravity estimate **0.85**
 Average Age 29

The skeletal restoration is based primarily upon a large juvenile or adult female ... Combining this specimen with others ... allowed the trunk and limbs to be accurately restored in all views, except for the number of dorsals. A large skull was scaled down to fit, and the incomplete neck was proportioned according to one partial vertebrae relative to its limb elements, and the breadth of the articulations in dorsal view. Restored flesh shoulder height is nearly 3.8 m. The biggest remains (two giant neck vertebrae and a partial central metacarpal) suggest males reached about 4.8 m. The completed restoration is neither as heavy in appearance as that published by Granger & Gregory, nor as extremely gracile as the Russian mount (Gromova, 1959). Granger & Gregory overscaled most of their classic figure (femur and vertebral column too long, hip too large), and placed the shoulder joint too low on the chest, making it too tall at 5.25 m. The mounted skeleton's errors (neck too long, pelvis too small, ribs too short, feet and humerus too long relative to femur, limbs too vertical) mainly stem from being made up of bones from individuals of different size (an example of the failure to cross-scale elements to a common size!). Because the new restoration has a very broad ribcage and hips, it is unlikely that the volume is too low. Neck musculature is restored as deep yet narrow, as in other ungulates. The massive abdomen is given a simple rhino-like semi-circular lateral profile. Limb musculature is restored as proximally powerful and distally light as per modern flexed limbed ungulates, using moderately fast rhinos, camels and workhorses as models. Mass for the medium sized specimen is restored as 7.8 tonnes, of which 10% is in the head and neck. The similarity in the size of the bodies of the tall rhino and the mammoth of the same mass confirms the accuracy of this result (indricotheres also share a similar mass/shoulder height relationship with proboscideans). Assuming isometry the biggest bulls should have exceeded about 16.4 tonnes, but this may be somewhat conservative since ungulates tend to become more massive relative to their neck and legs as they mature (Damuth & MacFadden, 1990). "World record" specimens are predicted to have reached 6 m and 30 tonnes. The results are in general agreement with the bone dimension/mass scaling calculations of Gingerich (1990) and Fortelius & Kappelman (1993), which offers further evidence of the accuracy of mass estimates based on technical data. Taken together, these studies also contradict extreme estimates of the size of known specimens. In particular, Alexander's (1989) 34 tonne mass estimate is too high because the trunk length (from Granger & Gregory, 1936) on which he based this estimate is excessive."

Alexander's 34 tonne mass estimate was also too high because it was based on the larger Grade I animal. The smaller size calculated by Paul indicates the shoulder height should be 4.8 metre instead of the original 5.25 metre tall estimate of Granger & Gregory (1936). Using Alexander's method to calculate a mass estimate for this reduced height animal gives $33.2 \times (4.8/5.25)^3 = 25.4$ tonnes. Paul's reconstruction also seems to have a shorter body length and the combination of this shorter body length of 0.97 reduces the mass further to $25.4 \times 0.97^3 = 23.2$ tonne (assuming the reduced length also affects the other dimensions). Thus envisioning the largest animal as a buffalo shaped animal (23.2 tonne) like Granger & Gregory (1936), instead of a more slender animal (16.4 tonne) like Paul (1997) makes less difference than changing the reconstructed size.

Prothero (2013, p105) also seems to believe that a "15 – 20 tonne estimate for the biggest indricotheres" is a more realistic than previous estimates in the 30 tonne range.

Larramendi (2015) used the GDI method based on Paul's (1997) reconstruction, producing a very similar body mass of 17.4 tonnes. He tells us that a "body mass of around 17 tonnes is therefore expected for the largest *Paraceratherium* bulls."

Gingerich (1990) predicted the body mass of a smaller "*Baluchitherium*" as 9 tonne using a range of long bone lengths and diameters and about 14-15 tonnes for the largest specimens. These calculations were rather involved but they didn't use any model or skeletal reconstruction of the completed animal.

A commercially available *Paraceratherium* model produced by CollectA was scaled to both the Grade II and the Grade IV specimens (see Figure 1). The dimensions calculated by Paul (1997) for the living animals indicated that the scales were 1/45 for the Grade II specimen and 1/37.5 for the Grade IV specimen. Using the basic technique outlined in Alexander (1989) the model volume was used to determine the living mass of both specimens. With an average tissue density of 0.97 tonne cu.m the mass for the Grade II specimen was 17.3 tonne, while the mass of the Grade II specimen was just under 10 tonne.

Palaeontologists generally seem to agree that the mass of the larger specimen of *Paraceratherium* would be between 15 to 20 tonnes. The commercially available *Paraceratherium* model also indicates masses which seem to agree with this general consensus. Taking all this evidence together, a mass of 17 tonne was chosen as the most reliable estimate for the largest specimen,

while the best estimate for the smaller specimens were taken as 10.5 tonne.

4. Weight from bone dimensions

The weight of the *Paraceratherium transouralicum* specimens can be directly calculated from the dimensions of their leg bones. The standard metric unit for weight is newton but the incorrect unit of kg or tonne has been widely used in most previous studies. Weight has been highlighted as a force by denoting weight as either kg(f) or tonne(f). A kg(f) force would be multiplied by 9.81 to convert it to the standard metric unit of newton.

Anderson *et al* (1985) studied the bones of a range of mammals to see if there were any rules that would allow them to estimate the weight of an animal from just its leg bones. This would be very useful for extinct animals such as dinosaurs.

The Anderson team chose to study the major leg bones which are often well preserved in otherwise incomplete fossils. A good indication of the weight of present-day animals is the circumference of the upper leg bones – the humerus and the femur. The bones were measured where they were the thinnest, and so the weakest, usually about half way along the length of the bones. These two circumferences were then added together to give the total circumference.

The Anderson team used statistical analysis to define the equation for a quadrupedal animal:

$$W = 0.000084.c^{2.73}$$

where: W = body weight in kg(f), and c = total of humerus and femur circumference in mm.

One use of these equations would be to calculate the weight of extinct animals and the Anderson team applied their equations to a number of dinosaurs.

Most dinosaurs should have been close to the best fit line, and certainly within $\pm 30\%$, but the calculated results indicated dinosaurs that were much lighter than anyone had ever thought possible.

Since the bone results were published in 1985 the mass of dinosaurs based on volume methods have been reduced to try to agree with these super-light-weight estimates for dinosaurs. Since the two methods give very different results some palaeontologists, as noted previously for Hutchinson *et al* (2007), advised abandoning the use of the formula based on leg bones entirely, since they cannot get dinosaurs' mass small enough to agree with the bone weight calculations. These types of criticisms encouraged Campione *et al* (2012) to slightly modify the original Anderson *et al* (1985) formula to produce increased weight estimates for larger dinosaurs more in line with the volume mass estimates.

Estimates of a quadrupedal animal's weight (*w*) can be calculated from the combined circumference (*c*) of their humerus and femur leg bones using the formula derived by Anderson *et al.* (1985).

Granger & Gregory (1936, p38-40) provided comparative measurements of limb bones from a variety of specimens. Some bones were not recovered so they estimated these based primarily on associated parts. There was a complete fossil of a Grade II humerus (No 26166) and a Grade IV Femur (No 21618). Some of the fossil specimens of the "*Baluchitherium osborni*" provided by Forster-Cooper were almost identical to a Grade IV fossil (No 26169) specimen so these were assumed to be from a similarly sized animal. These British specimens are now housed in the Natural History Museum in London.

Since the dimensions of the Grade I specimen were estimated from just a large jaw bone fossil it is generally considered unreliable. The Grade II and the

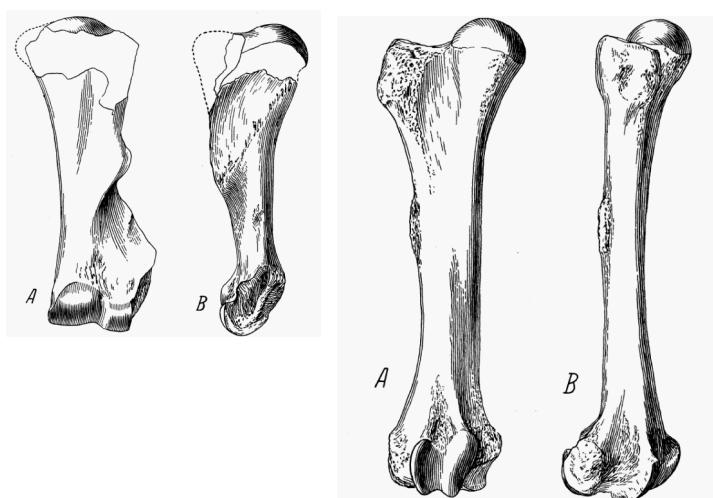


Figure 3.

The humerus and femur restoration of *Baluchitherium* (*Paraceratherium*) provided in Granger & Gregory (1936, Fig. 23 & 28). Both restorations show the anterior (A) and lateral view (B). The humerus was from a large animal - Grade II. The femur was from a small animal - Grade IV.

Grade IV specimens have better confirmation. Weight estimates are based on circumferences calculated from dimensions of the leg bone illustrations given in Granger & Gregory (1936) for the No 26166 specimen (Grade II) and the No 26169 specimen (Grade IVa). The circumference of the Humerus of the British specimen (Grade IVb) was calculated from the illustration in Forster-Cooper (1923) while the Femur circumference was measured directly from the specimen housed at the Natural History Museum (personal communication from N. Gabriel). It was also noted that this femur specimen was also identified as a Proboscidean by the Natural History Museum.

5. Palaeogravity

Palaeogravity was calculated using the standard formula previously described:

$$g_{29} = w_{29} / m$$

Palaeogravity for the large *Paraceratherium transouralicum* Grade II specimen was estimated as 0.73g, while the two smaller specimens, Grade IVa and IVb, were 0.81g and 0.85g at approximately 29 million years ago.

6. Accuracy

Many of specimens of *Paraceratherium transouralicum* are incomplete so reconstructions of this animal have relied on comparisons between different specimens to form composite animals. There even seems to be some doubt whether some specimens (such as the British femur) have been correctly identified. Although it was also noted that the Grade II and Grade IV specimens seem to give slightly different values of palaeogravity there are insufficient specimens to determine if this is a real difference or merely scatter. A tentative suggestion is that female specimens would carry extra weight due to child rearing - presumably this might be verifiable since it should also be true for mammals of today. Because of these uncertainties all three calculations have only tentatively been placed in a $\pm 20\%$ accuracy band.

7. Suggested Citing Format

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8. Publication History

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