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Shoulder height, body mass, and shape of proboscideans

ASIER LARRAMENDI

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In recent decades there has been a growing interest in proboscideans' body size, given that mass is highly correlated with biological functions. Different allometric equations have been proposed in the recent decades to estimate their body masses, based on a large number of living examples. However, the results obtained by these formulae are not accurate because extinct animals often had different body proportions and some were outside the size range of extant samples. Here the body mass of a large number of extinct proboscideans has been calculated by the Graphic Double Integration volumetric method which is based on technical restorations from graphical reconstructions of fossils employing photos, measurements and comparative anatomy of extant forms. The method has been tested on extant elephants with highly accurate results. The reconstructions necessary to apply this method give important information such as body proportions. On the other hand, equations to calculate the skeletal shoulder height have been developed, with a large number of published shoulder heights being recalculated. From the shoulder heights, several equations were created to find out the body mass of a series of extant and extinct species. A few of the largest proboscideans, namely *Mammut borsoni* and *Palaeoloxodon namadicus*, were found out to have reached and surpassed the body size of the largest indricotheres. Bearing this in mind, the largest land mammal that ever existed seems to be within the order of Proboscidea, contrary to previous understanding.

Key words: Mammalia, Proboscidea, *Mammuthus*, *Palaeoloxodon*, *Deinotherium*, body mass, shoulder height.

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Introduction

Over 60 million years of evolutionary history, the order Proboscidea produced animals of a wide size range, from a few kilograms in the earliest representatives, to several times larger than extant forms. The morphological variation and appearance among different families and genera was also remarkable.

Body size has an important impact on the physiology, morphology, diet, metabolic rate, gestation time, home range size, and fitness of all mammals' (Damuth and MacFadden 1990; McNab 1990; Roth 1990; Christiansen 2004; Kingsolver and Huey 2008). Several methodologies for estimating the body mass of extinct proboscideans have been proposed (Roth 1990; Shipman 1992; Paul 1997; Fariña et al. 1998; Christiansen 2004; Palombo and Giovinazzo 2005; Athanassiou 2011; Larramendi 2014). Most of these methods are based on bone dimensions; they rely on deriving allometric scaling formulae from a large number of living examples and these formulae are then used to estimate body mass for fossil forms. These methods could be problematic because extinct forms were often much smaller or larger than extant elephants and may have had different body proportions and significant differences in body mass/bone dimension relationships (Haynes 1991; Paul 1997; Larramendi 2014). Another problem with allometric formulae is that they are often based on captive elephants with body masses much higher than those observed in the wild with comparable shoulder heights.

A popular technique based on compiling data on the body mass and shoulder height of living elephant populations, to derive predictive equations and applying these to the calculated live shoulder heights of extinct taxa, is very common (Fortelius and Kappelman 1993; Ferretti 2007, 2010; Lister and Stuart 2010; Palombo et al. 2010; Athanassiou 2011) because it is well known that among extant species there is a close relationship between shoulder height and body mass (Laws 1966; Hanks 1972; Laws et al. 1975; Roth 1990). However, this method is very questionable due to the significantly different body proportions of most extinct forms (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Larramendi_SOM.pdf). Also, there appears to be important errors in most

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of the published shoulder heights because they are based on inaccurately mounted skeletons that often are mounted with the scapulae very low on the chest, which makes the skeleton too tall. Moreover, some authors apply an incorrect bone length to the shoulder height ratio (Larramendi 2014). Nowadays, the volumetric method is regarded as a more accurate method than the allometric one, especially when based on rigorous skeletal reconstructions (physical or digital) from complete specimens. It is thus increasingly used (Haynes 1991; Paul 1997; Hurlburt 1999; Motani 2001; Murray and Vickers-Rich 2004; Lovelace et al. 2007; Bates et al. 2009; Taylor 2009; Hutchinson et al. 2011a; Larramendi 2014). Accordingly, for this study, many extinct species have been restored volumetrically from the best preserved and available data.

There are several aims to this study: revise published shoulder heights, develop methods to calculate shoulder heights accurately, ascertain the body size of extant elephants in good condition, find out the body mass and shoulder heights of different extinct species, determine their average and maximum size and create equations to calculate body mass from the shoulder heights of a number of different proboscidean species based on body masses and allometric growth calculated in this paper.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CPSGM, Collections paléontologiques du Service Géologique du Maroc, Direction de la Géologie, Ministère de l'Energie et des Mines, Rabat, Morocco; DMNH, Denver Museum of Nature and Science, Denver, USA; FMNH, Field Museum of Natural History, Chicago, USA; GSI, Museum Geological Survey of India, C.R., Nagpur, India; IGF, Museum of Geology and Paleontology of the University of Florence, Florence, Italy; KNM, Kenya National Museum, Nairobi, Kenya; MBMa, Fossil mammal collection, Natural History Museum, Berlin, Germany; MECN, Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; M.F.P.S., Murchison Falls Park South, Lolim, Uganda; MNHM, Naturhistorisches Museum Mainz, Mainz, Germany; MNHN, Muséum national d'histoire naturelle, Paris, France; MPG, Museum of Paleontology of Guadalajara, Guadalajara, Mexico; MWNH, Museum Wiesbaden Natural History Collections, Wiesbaden; NHMW, Naturhistorisches Museum in Wien, Wien, Austria; NMC, National Museums of Canada, Ottawa, Canada; NMNS, National Museum of Natural Science, Taichung, Taiwan; RGM, Naturalis Biodiversity Center, Leiden, The Netherlands; SBV, Geological Museum of Shaanxi, Xi'an, China; UF, University of Florida, Gainesville, USA; UNSM, University of Nebraska State Museum, Lincoln, USA; USNM, National Museum of Natural History, Washington, D.C., USA.

Other abbreviations.—GDI, Graphic Double Integration; PE, prediction error; SG, specific gravity; (s)SH, (skeletal) shoulder height; WD, water displacement.

Material and methods

Twenty-four different species of proboscideans were technically restored (see Appendix 1). In order to do so, the best-preserved specimens from partially to nearly complete skeletons were selected to get the best results. When one particular specimen was nearly complete except for a few parts of the skeleton that were missing, the complete restoration was carried out by comparing similar-sized specimens of the same species where those missing parts were preserved. For each restored specimen, descriptions, bone measurements, photographs and illustrations were obtained first, mainly from the bibliography. Some measurements were collected personally and taken with sliding callipers or flexible tape. The postcranial measurements were carried out in accordance with Göhlich (1998) and with additions from Lister (1996). The reconstructions were made bone by bone, adding flesh carefully, applying comparative anatomy of extant proboscideans. To get the most rigorous results, the restorations were done in a vector graphics editor where one millimetre was equated to one pixel; thus, a real humerus of 1320 mm in length was restored in 1320 pixels. The volumes of the different restorations were estimated using Graphic Double Integration (Jerison 1973; Hurlburt 1999; Murray and Vickers-Rich 2004), which was applied in MATLAB and where each model was checked pixel by pixel. Specific gravities varying from 0.99 to 1.05 were applied to the models to get the body masses (see below). The body masses calculated for 108 different specimens (SOM: table 2) were based on the extrapolation of the results obtained from the volumetric restorations, taking into account the body proportions of the studied specimens from appendicular bone measurements. To help to know if the studied specimens were still growing animals, the age of the specimens was determined by the state of wear and eruption of the molars, in accordance with Laws (1966) and Jachmann (1988), averaged across the preserved molars and based on the average body masses calculated for different species. The skin surfaces were calculated from restored animals, treating them as elliptical cylinders. We have very few data on the height and body mass relationship from animals whose size is above the average. The only such data from mammals available is that of humans. Thus, the relationship between height and body mass of 561 *Homo sapiens* individuals of different heights—from low average (170 cm) to 25% taller than average (225 cm) was studied in order to help to find out approximate growth curve for proboscideans much taller than average and obtain their size limit. The data were collected from the official NBA website; most of the info came from the players of the 2013–2014 season and this was supplemented with players from other seasons, in a bid to obtain the data on the tallest humans. The data of this study consist of the shoulder heights (in cm), body masses (in kg and tonnes), bone measurements (in mm), body volumes (in ml and m^3), and skin surfaces (in cm^2 and m^3). Most of the older publications do not usually specify the humerus length (articular or maximum), but rather refer to articular length. Thus, any doubtful length was treated as articular length in this study. When a humerus length is listed in this paper just as "humerus length", it refers to articular length, the distance from the caput to the distal articular surface. In this paper, the term "mastodont" refers to mammutids and gomphotheres.

Shoulder height: skeletal and in the flesh

Larramendi (2014) dealt with the existing problem of the definition and calculation of shoulder height. Skeletal shoulder heights of extinct proboscideans have usually been calculated or measured including the spines of the thoracic vertebrae above the scapulae (Christiansen 2004; Kosintsev et al. 2004; Lister and Stuart 2010; Baigusheva et al. 2011). This may be because nearly all mounted skeletons have the backbones above the scapula, but as Larramendi (2014) pointed out, this is is not rigorous if one observes walking elephants of both genera one will see the scapulae rising and lowering several centimetres above the spines as they walk. Due the fact that Elephantiformes and Plesielephantiformes had similar scapular shape, comparable forelimb structure and similar first thoracic vertebrae composition, it is likely that all proboscideans had the dorsal border of their scapulae just above the dorsal extremity of neural spines of the anterior thoracic vertebrae. Skeletal shoulder height, therefore, should be measured or calculated only to the top of the scapula.

The best way to calculate the skeletal shoulder height (sSH) of an extinct proboscidean from a complete preserved forelimb, is to restore it digitally in the anatomical position on the basis of measurements and photographs (Larramendi 2014). Another easy technique for finding the skeletal shoulder height of proboscideans is to add up the articular or maximum lengths of the thoracic limb bones minus a few per cent (Fig. 1). As observed in the restorations from Appendix 1, in derived proboscideans (Elephantidae) where the forelimbs are nearly columnar, the SH can be obtained by adding the articular or physiological lengths of the scapula, humerus, ulna and manus height and multiplying the result by 0.98 (see Fig. 1). If one wanted to calculate the sSH from the maximal lengths of the scapula, humerus, radius plus manus height, the result obtained by adding up these lengths should be multiplied by 0.95 (see Fig. 1). For more archaic proboscideans within Mammutoidea, Gomphotherioidea or Elephantoidea, where the forelimbs are somewhat more flexed, the results should be multiplied by 0.97 and 0.94, respectively.

Manus height is usually very difficult to obtain. The main reason for this is that it is rarely correctly mounted; often manus are mounted too flat or sometimes they are positioned too vertically (the manus of proboscideans within Elephantiformes and some Plesielephantiformes can be described as subunguligrade [Trevisan 1949: fig. 43; Miller et al. 2008; Hutchinson et al. 2011b]) and usually manus elements are missing. However, the restored manus of different species from the Appendix 1 indicate that multiplying the third metacarpal length by 2, in the case of derived proboscideans (elephants and stegodonts), and by 1.75, in most of mammutids and gomphotheres, the manus height can be accurately calculated (Tables 1, 2). The third metacarpal length usually represents the 25% of the radius length in the case of most proboscideans (Elephantimorpha and *Prodeinotherium*), and around 30% in *Deinotherium*. The shoulder height and the body mass can thus be easily calculated from the third metacarpal in proboscideans (see

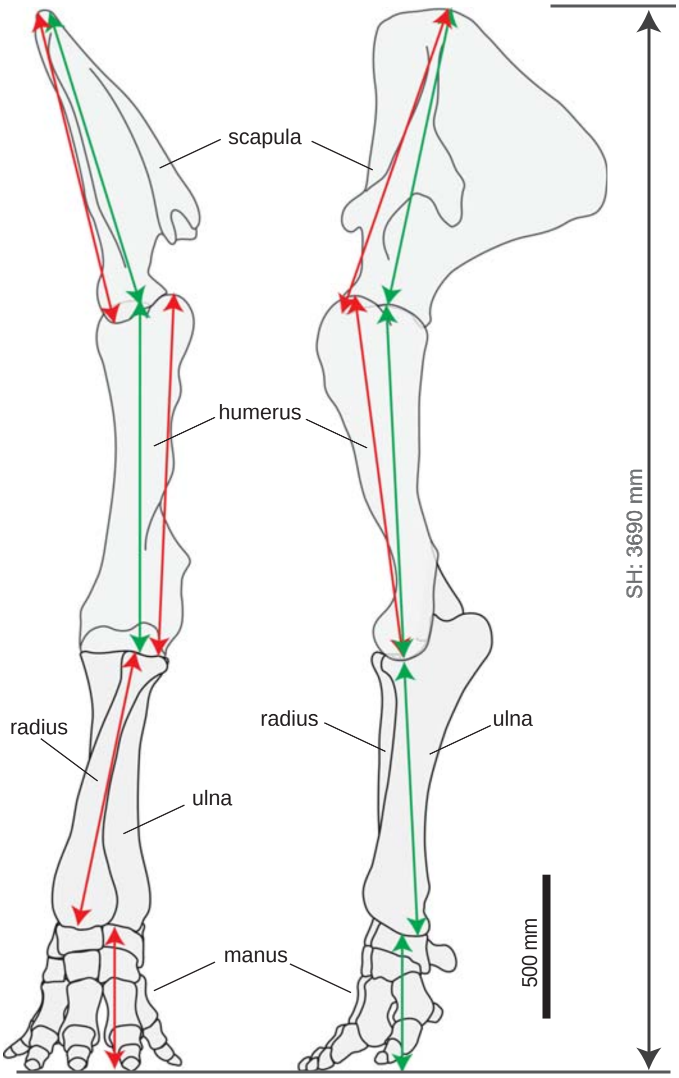

Fig. 1. Reconstruction of the forelimb of the Zhalainuoer III mammoth in anatomical position. The actual shoulder height (black): total height in anatomical position 3690 mm. The height obtained by adding the articular (green): manus (500 mm) + ulna (960 mm) + humerus (1233 mm) + scapula (1075 mm) = 3768 mm. Maximal lengths of different bone elements (red): manus (500 mm) + radius (985 mm) + humerus (1274 mm) + scapula (1115 mm) = 3874 mm. The actual shoulder height can be calculated by multiplying the result by 0.98 in the case of the sum of articular lengths and by 0.95 in the case of maximal lengths.

Table 1. Ratios between manus height vs. metacarpal (MTC) III length for different proboscidean species. Skeletal manus heights obtained from the restorations of the Appendix 1.

Species	Individual	MTC III length (mm)	Manus height (mm)	Manus height vs. MTC III length ratio
Mammuthus trogontherii	Zhalainuoer III	255	500	1.98
Mammuthus meridionalis	Scoppito	266	525	1.97
Mammut americanum	Warren	~170	305	1.79
Palaeoloxodon antiquus	Viterbo	248	490	1.97
Gomphotherium productum	DMNH 1261	171	295	1.73
Gomphotherium steinheimense	Mühldorf	221	455	2.06

below). In case the third metacarpal is not preserved, the manus height can be calculated from the maximum radius length. In derived proboscideans, the manus height represents usually about 50% of the maximum radius length, or about 45% in the case of most of mammutids and gomphotheres and nearly 60% in deinotheres (Table 2). *Deinotherium* has very elongated metacarpals and had the tallest manus among Proboscidea. If the radius is not preserved but the ulna is, then the manus height can be calculated from the articular length of the ulna applying the same percentages mentioned for the radius above, but the results will not be so accurate because the ulna articular length is slightly less than radius length. A considerable error in calculation of manus height will not affect significantly the total sSH calculation because the manus represents the shortest part of the forelimb. Therefore a calculation error of 10% on manus height would only affect the total sSH by about 1%.

Most of the published shoulder heights are inaccurate, principally because the skeletal shoulder heights were obtained from incorrectly mounted skeletons, usually with the scapulae too low in the chest, making the skeletons too tall. Therefore, many of the published sSH have been recalculated in the manner mentioned above (SOM: table 2).

Unfortunately, on many occasions, only isolated limb bone elements are found. Hence, appendicular bone lengths/skeletal shoulder height ratios have been obtained for several derived extinct proboscideans (*Palaeoloxodon antiquus*, *Mammuthus meridionalis*, *M. trogontherii*, *M. columbi*, *M. primigenius*) from the data collected in this study (Appendix 1, SOM: table 2). The results (Table 3, Figs. 2–8) differ from the calculated ratios and percentages of the appendicular bone lengths related to the shoulder height from published studies (Harington et al. 1974; Shpansky et al. 2008; Lister and Stuart 2010; Athanassiou 2011; Baigusheva et al. 2011). The reason is that, as mentioned above, the published shoulder heights of different mounted skeletons are not reliable. It is worth noting that in the tallest mammoths, the sSH/femur ratio tends to increase approaching 2.6 (~0.08 more than average), which causes a more pronounced sloping back in very large and generally old specimens, making the tallest mammoths less heavy relative to their shoulder heights compared to smaller specimens and species.

Shoulder heights would have been greater in the flesh. Larramendi (2014) studied this subject in depth and found that proboscideans in life are about 5.5% taller than their sSH after taking into account the skin, soft tissues, muscles and cartilage. Similar percentages have been applied in different works (Osborn 1942; Lister and Stuart 2010;

Table 2. Ratios between metacarpal (MTC) III length vs. radius length and manus height vs. radius length of different proboscidean species. Skeletal manus heights are calculated based on the ratios obtained from Table 1 and Appendix 1, where the manus height vs. MTC III ratio is very close to 2 in case of derived proboscideans and deinotheres, and 1.75 in case of most mastodonts.

Species	Individual	MTC III length (mm)	Radius length (mm)	Calculated manus height (mm)	MTC III length vs. radius length (%)	Manus heigth vs. radius length (%)
Mammuthus primigenius	Pfannerhall	208	825	416	25.2	50.4
Mammuthus primigenius fraasi	Steinheim	245	955	490	25.7	51.3
Mammuthus trogontherii	Zhalainuoer III	255	985	500	25.9	51.8
Mammuthus meridionalis	Scoppito	266	950	525	28	55.3
Mammuthus meridionalis	Nogaisk	265	1040	530	25.5	51
Mammuthus columbi	MSL-140	237	948	474	25	50
Mammuthus columbi	NSM1597-62-2	194	823	388	23.6	47.2
Mammuthus columbi	SDSM 124688	244	928	488	26.3	52.6
Mammut americanum	Watkins Glen	171	690	299	24.8	43.5
Palaeoloxodon antiquus	Upnor	246	990	492	24.8	49.6
Palaeoloxodon antiquus	Konin	252	1002	504	25.1	50.2
Palaeoloxodon antiquus	II Crocifisso	205	805	410	25.5	51
Deinotherium levius	Gussiantin	280	965	560	29	58
Deinotherium proavum	Obukhovka	274	950	548	28.5	57.7
Gomphotherium productum	DMNH 1261	171	648	295	26.4	45.5
Gomphotherium steinheimense	Mühldorf	221	840	455	26.3	54.2

Lister et al. 2012). All the restored animals (see Appendix 1) were increased by a very similar percentge to that proposed by Larramendi (2014), and a factor of 1.055 was applied to the sSH in order to estimate shoulder heights in the flesh in SOM: table 2.

Body mass estimations

Allometric method

An often-used method to calculate the body mass of extinct proboscideans is to derive an allometric scaling formula from a large number of living examples and to apply it to the fossil form (see Roth 1990; Shipman 1992; Christiansen 2004; Ferretti 2007; Lister and Stuart 2010; Marano and Palombo 2013). Allometric methods have several problems, especially with extinct forms. In this case, extinct proboscideans were often larger than extant elephants, and many of them had different body proportions and significant differences in the relationship between body mass and bone dimension (Haynes 1991; Larramendi 2014). The most rigorous and most widely used work to date aimed at finding the body masses of proboscideans by the allometric method is probably Christiansen's (2004) study. He developed several formulae based on regression analyses of limb bone dimensions relative to body mass, for seven female specimens of modern elephants (three *Loxodonta africana* and four *Elephas maximus*), for which body masses were recorded prior to death.

According to these formulae, the estimated average body mass of the famous Jumbo African elephant (AMNH 3283) is about 7.6 tonnes (Table 3). This result notably differs from the estimated body mass of wild elephants of Jumbo's shoulder height (323 cm; Appendix 1: R) by about 1.5 tonnes (Laws 1968; Hanks 1972). On the other hand, the body mass obtained for NMNS002990-F002715 a female skeleton of *L. africana*, with a calculated shoulder height in the flesh of 253 cm, is 3.5 tonnes, about 750 kg or 27% more than expected for a non-pregnant female African elephant of this height in good condition (see Table 4; SOM: table 1). It is likely that the problem lies in the fact that six of the individuals in the selected sample were captive animals and weighed around 3.5 tonnes or more (Christiansen 2004). These body masses are considerably more than those observed in the wild for both extant genera, where female individuals rarely surpass 3 tonnes (Laws 1966; Laws and Parker 1968; Laws et al. 1975; Kurt and Kumarasinghe 1998). Finally, there is considerable variation in the mass predictions from different bones, the results vary by over 80% in a single individual (see Christiansen 2004; SOM: table 1). Therefore, they are not convincing for estimating body mass of extant or extinct forms.

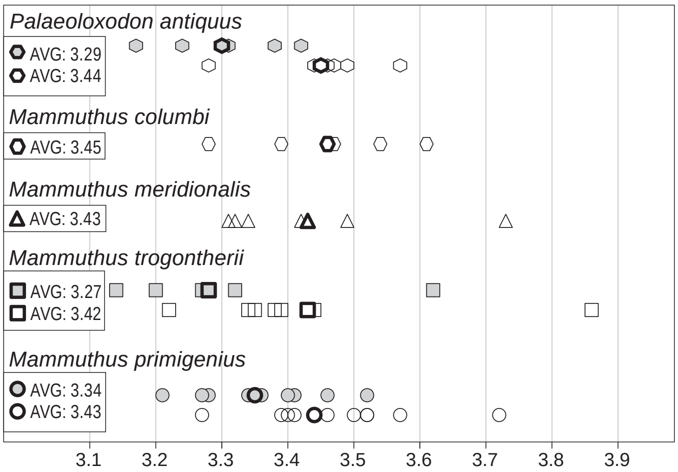

Fig. 2. Scapula lengths vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data). The ratios shaded in grey correspond to the maximal length of the scapula and the white ones to the articular length of the scapula.

Volumetric method

The volumetric method requires creating a physical or digital model of an animal to find out its volume, multiplying by a scale factor to get the volume of the animal in life and applying the estimated density of the living animal to get its mass. Many authors have used this method to calculate the body mass of extinct forms, especially of dinosaurs (Paul 1988, 1997; Gunga et al. 1995, 2007, 2008; Hurlburt 1999; Motani 2001; Murray and Vickers-Rich 2004; Lovelace et

Table 3. Different proboscidean species ratios/percentages of different appendicular skeleton bone lengths vs. skeletal shoulder height.

Element of measure	*Mammuthus primigenius*	*Mammuthus columbi*	*Mammuthus trogontherii*	*Mammuthus meridionalis*	*Palaeoloxodon antiquus*
Scapula maximal length	3.34/29.94%	–	3.28/30.49%	–	3.29/30.4%
Scapula articular length	3.43/29.15%	3.45/28.99%	3.42/29.24%	3.43/29.15%	3.48/28.74%
Humerus maximal length	2.91/34.36%	2.86/34.97%	2.91/34.36%	2.88/34.72%	2.83/35.34%
Humerus articular length	2.98/33.55%	2.98/33.56%	2.97/33.67%	2.94/34.01%	2.95/33.9%
Ulna maximal length	3.40/29.41%	3.39/29.5%	3.38/29.59%	3.32/30.12%	3.31/30.21%
Ulna articular length	3.90/25.64%	–	3.95/25.32%	3.88/25.77%	3.97/25.19%
Radius	3.75/26.67%	3.69/27.1%	3.81/26.25%	3.84/26.04%	3.73/26.81%
Femur	2.44/40.98%	2.56/39.06%	2.53/39.53%	2.52/39.68%	2.56/39.06%
Tibia	4.31/23.2%	4.36/22.94%	4.3/23.26%	4.32/23.15%	4.15/24.1%
Fibula	4.46/22.42%	4.37/22.88%	4.47/22.37%	4.49/22.27%	4.31/23.2%

Table 4. Comparison between the allometric (Christiansen 2004) and volumetric (this paper) method for estimation of body mass from a selected sample of different proboscideans. Note that some specimens are either much heavier or lighter than predicted by the volumetric method.

Species	Individual	Estimated body mass —allometric (kg)	Estimated body mass —volumetric (kg)	Discrepancy (%)
Mammuthus meridionalis	Scoppito	13 207	10 744	22.92
Mammuthus trogontherii	Zhalainuoer III	10 029	10 435	-4.05
Mammuthus trogontherii	Azov I	12 705	11 500	9.5
Mammuthus primigenius	Siegsdorf	8041	8241	-2.49
Mammuthus primigenius	Rottweil	3794	~3000	26.47
Mammuthus exilis	1994	1722	1347	27.84
Mammut americanum	K, Kolarik	4828	~6500	-34.63
Stegodon zdanskyi	Yellow River	12 240	12 739	-4.08
Gomphotherium steinheimense	Mülhdorf	7169	6682	7.29
Loxodonta africana	AMNH 3283	7464	6146	21.44
Loxodonta africana	NMNS002990–F002715	3465	2709	27.9
Palaeoloxodon antiquus	Konin	12 308	~11 500	4.68

al. 2007; Bates et al. 2009; Taylor 2009; Hutchinson et al. 2011a; Larramendi 2014).

The main problem with this method is that usually extinct forms are known from only a few remains to produce a good restoration. To get the best and most accurate results, it is very important to base the reconstructions on the best preserved and most complete available specimen. The model must also be adjusted as closely as possible to the original skeleton (Paul 1997). Proper documentation—such as descriptions, measurements, photographs, illustrations, etc.—of the skeleton is also necessary.

Comparative anatomy.—The use of modern analogues, living animals that are most like extinct forms, are very important to restoring extinct animals (Paul and Chase 1989). Fortunately, extant proboscideans, are very helpful for this study. Many studies of hard and soft anatomy on living elephants have been carried out over recent centuries (Cuvier 1849; Watson 1872a, b, 1874, 1875; Boas and Paulli 1925; Eales 1926; Shindo and Mori 1956a–c; Shoshani et al. 1982; Shoshani 1996; Shoshani and Marchant 2001; Marchant and Shoshani 2007) and have been used as a guideline. Photographs (especially direct lateral and aerial views) and films are also very important because they allow the bones and skin to be placed correctly. Walking elephants have been personally filmed for further help. A small space (just a few mm) between vertebrae and between limb bones must be added for the cartilages. As the musculature of extant elephants is very well known, the gross superficial musculature could be accurately applied, profiling it in solid black as per Paul (1997).

Muscles and skin: The leg musculature has been carefully restored. Despite proboscideans' enormous weight, they do not have very developed limb musculature (Knight 1947; Haynes 1991; Paul 1997). However, the legs of deinotheres, mastodonts, stegodonts, and some elephantids such as *Palaeoloxodon antiquus* were clearly more heavily built. Special attention should be paid to the skull musculature. Both the extant genera *Loxodonta* and *Elephas* have the splenius muscle. This muscle inserts fanwise on the occipital ridge from the nuchal fossa downward over 3/4 of the posterior cranium (Eales 1926; Marchant and Shoshani 2007). This muscle is associated with head movements, such as shaking. *E. maximus* has an additional muscle lining the splenius (Marchant and Shoshani 2007). This extra muscle is known as the splenius superficialis or splenius capitis superficialis. The muscle helps to define the double-domed appearance of the Asian elephant head (Boas and Paulli 1925; Marchant and Shoshani 2007) and is probably associated with the taller and relatively large heads of Asian elephants that supply additional strength. It could also be an evolutionary adaptation related to the lifestyle and ecology of its ancestors. Therefore, all *Elephas* species probably had this muscle. The cranial morphology of *Elephas hysudricus* and *Elephas hysudrindicus* (Osborn 1942; Hooijer 1955) indicates that they must have had a very developed splenius superficialis muscle. Other extinct proboscideans, especially palaeoloxodonts, had very developed parieto-frontal crests, suitable for the insertions of this muscle. The splenius superficialis of these extinct elephants was probably much stronger than that of the extant *E. maximus*, contributing to an extremely developed double-domed shape (Appendix 1: V, W). Moreover, mammoths, with very high single-domed skulls, are predicted to also present this muscle (Marchant and Shoshani 2007). It is possible that the extra splenius muscle would help to balance the enormous, heavy, tusked heads. Hence, it is not feasible that most plesiomorphic proboscideans, such as *Moeritherium* and others (including deinotheres), present this muscle given the relatively flattened skulls that do not provide a sufficient insertion surface for this muscle. It is very difficult to predict whether the aforementioned muscle was present in mastodonts and other groups unless a rigorous osteological study is made species by species. Nonetheless, despite the enormous heads and tusks of mammutids, they probably do not present a splenius superficialis muscle, as their relatively low skulls and the absence of a developed occipital ridge make it un-

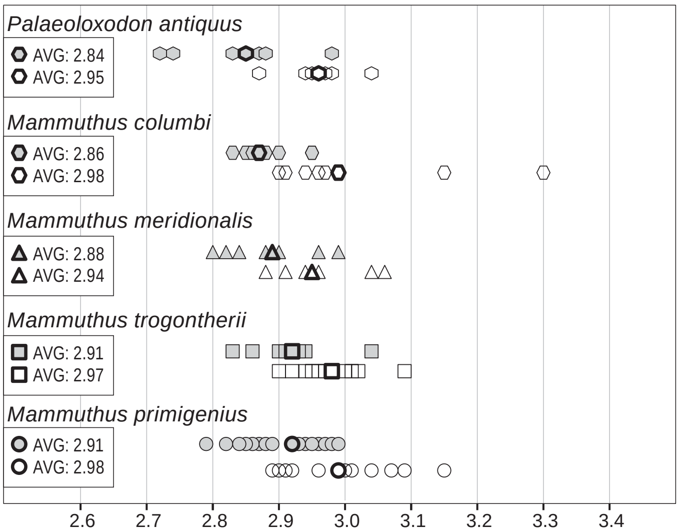

Fig. 3. Humerus lengths vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data). The ratios shaded in grey correspond to the maximal length of the humerus and the white ones to the articular length of the humerus.

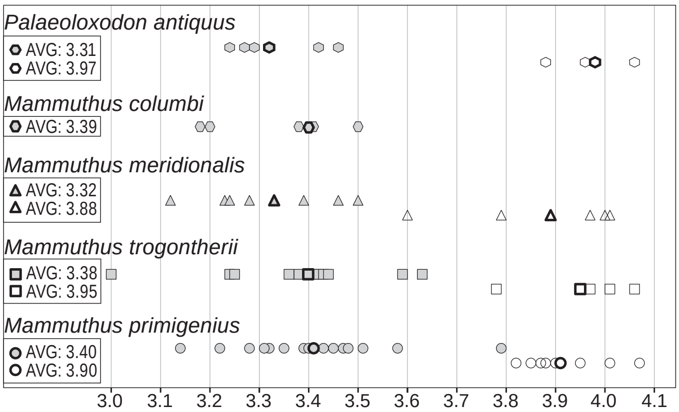

Fig. 4. Ulna lengths vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data). The ratios shaded in grey correspond to the maximal length of the humerus, and the white ones to the articular length of the humerus.

likely. Some gomphotheres (such as *Stegomastodon*) might have had the splenius superficialis muscle, while others not.

It is also important to not add too much flesh over the skeleton. The neural spines, ribs, dorsal part of the scapulae, olecranon process, iliac crest, and the anterior part of the tibiae are just under a few cm of skin on the elephants. The thinnest skin is on the trunk, ears, breast, groin, and legs (Sokolov and Sumina 1982), measuring about 10 mm thick on the medial leg (Shoshani et al. 1982), and the thickest skin of an extant elephant is on the back and can range from 30 to 40 mm (Shoshani et al. 1982; Skinner and Chimimba 2005; Larramendi 2014). Finally, the skin on the soles can be considerably thicker (Roth 1990; Haynes 1991; Christiansen 2004; Larramendi 2014). Therefore, the restored proboscideans' skin thickness in this study (depending on the overall size of each specimen) varies from 3 to 15 mm (on the thinnest parts), 7 to 45 mm (on the backs) and 10 to 60 mm (on the soles).

Trunks and ears: Some soft tissues such as the proboscis and ears of extinct proboscideans cannot be restored accurately (except for *Mammuthus primigenius*), although the size can be deduced. In elephants, as in all animals, different body parts evolve in concert, that is, they complement each other for the greatest efficiency in terms of energy conservation (Shoshani and Foley 2000). Thus, with regard to the trunks (proboscis), as most extinct proboscideans (Elephantiformes and deinotheres) had columnar forelimbs, the proboscis had to be long enough to reach the ground and facilitate feeding and drinking without bending. So when the neck and mandible are short and the legs are long, the trunk may be longer and vice versa. The cranial morphology, long neck, and long mandible of *Moeritherium* indicates that it did not have a proboscis, unlike many reconstructions. Markov et al. (2001) reconstructed a short tapir-like proboscis for *Deinotherium giganteum*, arguing that the skull did not provide sufficient insertion surface for a typical elephantine proboscis. The long neck and relatively long mandible of deinotheres also point to a short trunk, and it has been suggested that they might be capable of flexing the ulna to a greater extent than extant elephants (Harris 1973). However, it was probably not enough to reach the ground due to the very long forelimb elements. Therefore, a medium-length trunk is more plausible for this group of proboscideans. It is worth noting that the largest proboscis among proboscideans only represented about 2.5% of the total body mass and substantial errors in trunk volume estimations therefore barely affect the overall body mass estimation.

The size of the ears of extinct proboscideans can be roughly calculated on the basis of geographical distribution and interpretation of behaviour for each species, although the shape cannot be identified. For example, the cold-adapted woolly mammoth, *M. primigenius*, had human-like thick ears (up to 40 mm) of only about 30 cm in height, 537 cm^2 (one lateral side), and probably weighed less than 1 kg each, while today the savanna elephant has thin (up to 10 mm) ears of about 133 cm in height, 11 970 cm^2, and weighing 9 kg each (Shoshani 2000; Mol et al. 2006). On the other hand, the warm-adapted *Elephas maximus* has intermediate-sized ears of 6.5 kg each (Shoshani 2000). The European *Palaeoloxodon antiquus* probably had intermediate-sized ears relatively as big as the extant *E. maximus*, but the earlier *P. recki* from Africa might have had ears as large as the extant *Loxodonta africana.* The earliest representative of mammoths (*M. subplanifrons* and *M. africanavus*) lived in the tropics of Africa, and it is possible that their ears were much larger than in derived forms, as an adaptation for cooling the body (Haynes 1991). Other anatomical characteristics such as tail morphology and length could have a thermoregulatory function in a cold environment (Haynes 1991; Lister and Bahn 2007; Larramendi 2014) and may help us to interpret whether extinct forms were covered with fur or not and therefore their ear size too.

Graphic double integration method.—Paul (1997) and Hurlburt (1999) concluded that volumetric methods give more accurate results than other allometric methods. For this study, Graphic Double Integration (GDI) has been used to find out the body masses of the analysed proboscideans (Appendix 1). GDI is a volumetric method proposed by Jerison (1973) for estimating the volumes of endocasts from dorsal and lateral views. To determine the volume, the body or body part of an animal under research is modelled as an elliptical cylinder according to the following equation:

$$V= \pi(r_1)(r_2)(L)$$

where V is volume; r, radius; L, length.

The GDI assumes that all of the body segments of the model under investigation have elliptical cross sections, although this is not always true (Motani 2001). Fortunately, the rounded bodies of proboscideans are very suitable for applying this method and provide accurate results. This technique is quicker and easier than sculpting and displacing scale models and is as accurate as the Water Displacement (WD) method. For example, Jerison (1973) obtained a volume of 536 ml for a *Tyrannosaurus rex* endocast by GDI for which he determined a WD of 530 ml. In the case of proboscideans, the body mass calculated for the restored Jumbo elephant in this study is nearly equal (0.1 tonnes difference) to that produced by Paul (1997) by WD, although he applied a lower SG of 0.95 and the present model is just 5 cm taller, due to the fact that he made the scapulae too small. On the other hand, Larramendi (2014) used WD and GDI on the same model to calculate a Zhalainouer III mammoth body mass and discovered a difference of only 2% between the two methods.

Scale factor: It is important to explain how the volume or the mass increases between small and large things. If an object is isometrically increased by 25%, it does not mean that its volume will increase by a quarter; in fact, its volume will be nearly double that of the original. This is because the object will be 25% taller, 25% wider, and 25% longer ($1.25^3 = 1.95$). In other words, the volume, and therefore the mass, increases according to the cube of the size increases. This rule is used when converting the mass of a model to the original size. This concept can also translate to animals, when comparing individuals of different sizes, but it is necessary to take allometry into account (see below).

Specific gravity: Once the volume of any animal model is obtained, it is necessary to estimate the density in order to calculate the mass. Most extant land mammals have an overall density equal to that of water, although some land mammals sink and others float (Larramendi 2014). The overall density of any animal depends on the amount of air in their lungs because the density can vary by inflating and deflating them. So, to calculate or estimate the SG of any animal, it is important to consider a relaxed position that they would take, which is, naturally, the most common position of animals during their life (e.g., feeding, walking, sleeping).

Larramendi (2014) proposed a specific gravity of 0.99 for proboscideans after observing swimming elephants in a relaxed position. This density is also found in human beings. Humans barely float on fresh water in a relaxed position. However, most healthy humans, when they expel the tidal volume (or just a little more) of their lungs, which corresponds approximately to 0.7% (Beardsell et al. 2009) of the total body volume, tend to sink.

On the other hand, it must be taken into account that there are particulary dense land mammals, especially semi-aquatic ones. It is known that osteosclerosis in the appendicular skeleton is a common adaptation in semi-aquatic and aquatic mammals for buoyancy control (Wall 1983; Fish and Stein 1991; Coughlin and Fish 2009). Osteosclerosis is an increase in bone density by the replacement of cancellous bone with compact bone or by increasing cortical bone thickness at the expense of the medullary cavity, which increases the overall animal density (Wall 1983; Domning and de Buffrénil 1991; Coughlin and Fish 2009). This allows aquatic animals to walk along the bottom of rivers or lakes, for example, the hippos *Hippopotamus amphibius* and *Choeropsis liberiensis*, and the African mouse-deer, *Hyemoschus aquaticus* (Fish and Stein 1991; Coughlin and Fish 2009). These animals must have a density considerably higher than water, and hippos may be the densest land mammals; they are so dense that, in contrast to the African mouse-deer, they are probably not able to swim (Coughlin and Fish 2009). Therefore an SG of at least 1.10 is expected for hipos, and an SG probably between 1.01 and 1.05 for *Hyemoschus aquaticus.* It has been suggested that *Moeritherium* may have been a semi-aquatic animal (Matsumoto 1923; Osborn 1936), and a study based on *L. africana* embryos (Gaeth et al. 1999) suggests that elephants had aquatic ancestors. The overall morphology of moeritheres points to an aquatic lifestyle; the fairly complete quadrupedal sirenian skeleton *Pezosiren portelli* (Domning 2001) resembles very closely that of *Moeritherium lyonsi* (Appendix 1: A), with a very elongated body suitable for diving. Finally, an isotopic analysis of *Barytherium* and *Moeritherium* teeth suggests that these early proboscideans were semi-aquatic mammals that fed on freshwater vegetation in riverine or swampy settings (Liu et al. 2008). Therefore, it is expected that *Barytherium* and *Moeritherium* were denser than water. An SG of 1.05 was applied to the obtained volume in the *Moeritherium* restoration (Appendix 1: A) to calculate its body mass. Future histological analysis of *Moeritherium* and *Barytherum* will be of interest to find out their bone densities and confirm their aquatic specialization.

Other land mammals with non-aquatic habits, such as the nine-banded armadillo, *Dasypus novemcinctus* (Coughlin and Fish 2009), and American tapirs, *Tapirus bairdii* and *Tapirus terrestis* can walk underwater (AL personal observation). Videos of swimming Javan rhinoceros, *Rhinoceros sondaicus*, show that these animals can barely put their

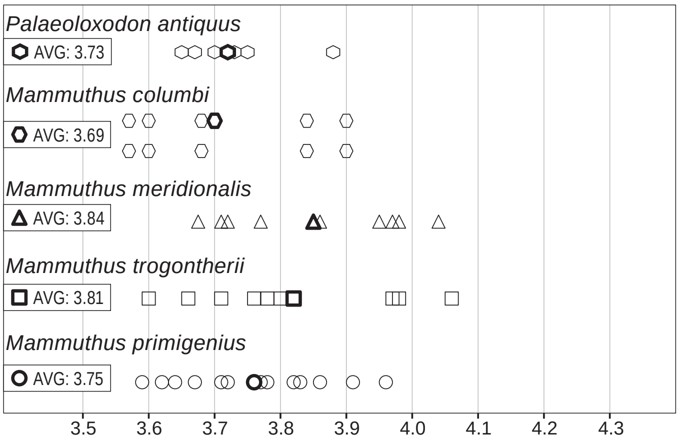

Fig. 5. Radius length vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data).

head above the water, indicating that the whole body would sink if it weren't for the leg movements that propel the body upwards. Therefore SGs over 1.0 are not only restricted to amphibious mammals. It is well known that many extinct forms, especially mastodonts, had much thicker limb bones, although mammoths might not have had more massive long-bone diaphyses on average than extant elephants (Christiansen 2007 contra Haynes 1991). Thus, thick limbs could have increased the overall density of mastodonts as compact bones (including long bones) could have an SG of about 2.0 (McGowan 1991; van Schalkwyk et al. 2004). Nevertheless, the main reason that the overall density of some extinct proboscideans was increased could have been the relation between skeletal mass and body mass. Many extinct proboscideans, especially plesiomorphic ones, had much more sturdily built skeletons than today's elephantids, even attaining similar body masses as extant forms. Thus, it is likely that most extinct forms had higher SGs than extant elephants; however, as it is not possible to calculate accurately the SG case by case, a conservative SG of 0.99 has been applied to the body volumes obtained in this study (except to *Moeritherium*). Moreover, the volume of tusks in some extinct proboscidean forms represented a significant percentage of the total body volume because of their relatively big sizes. The SG of mammoth and elephant ivory varies from 1.6 to 1.93 according to different studies (Kunz 1916; Schuhmacher et al. 2013; Yin et al. 2013). For this study an SG of 1.8 for tusks has been applied. The overall SGs of extinct proboscideans therefore vary from 0.99 to 1.01 depending on the tusk size of each studied specimen (Appendix 1).

Why did most extinct proboscideans have more massive bones than extant forms? One explanation could be that the sturdy limb bones of some proboscideans are possibly the result of the greater stress suffered in their bones due to more strenuous locomotor activity (Haynes 1991). However, the great resemblance of the appendicular skeletons of these massive extinct forms to those of extant elephants makes this suggestion unlikely because they don't show any significant signs of traits suggesting increased locomotor activity during their evolution (Christiansen 2007), although as will be discussed below, it should be noted that some dwarf-derived forms and deinotheres might show different locomotory adaptation compared to other archaic and modern proboscideans. Other explanations such as elastic similarity theory (McMahon 1973, 1975a, b) are hardly applicable in proboscideans because limb bone regression analyses have shown significant differences from elastic similarity (Alexander McNeill et al. 1979; Haynes 1991; Christiansen 2007).

A more convincing explanation (see also Christiansen 2007 for discussion) is that there is a very important factor accompanying size increase, namely the change in relative areas (Square-Cube Law). When an object or animal is scaled up, the volume increases at a much faster rate than the surface area (provided the object or the animal retain the same shape the volume will increase in cube and the surface in square). This principle has a great influence in all vertebrates, even when they are not very similar (Schmidt-Nielsen 1984). This implies that the stress suffered on the supporting point surfaces and in the bones of many extinct proboscideans such as mastodonts, deinotheres, stegodonts and European palaeoloxodonts was much higher than in extant elephants, because they were proportionally much heavier as they had considerably more elongated (in the case of mastodonts) and wider bodies. Therefore, extinct forms should have possessed thicker long bones to support their relatively higher body masses.

On the other hand, it is worth noting that extant elephants are probably the "slimmest" of all proboscidea. They present a smaller ratio between pelvis breadth and femur length (there could be some exceptions) than extinct forms, indicating that living elephants have relatively narrower bodies. For example, the ratio of extant elephants' (*Loxodonta africana* and *Elephas maximus*) greatest pelvis breadth usually is 1.0–1.15 of their femur length; in the case of mastodonts the ratio varies from 1.25 to 2.0 and the average ratio for mammoths is 1.2 (Appendix 1, SOM: table 2).

GDI accuracy: The accuracy of GDI was tested on two extant elephant species, *Elephas maximus* and *Loxodonta africana*. The mounted skeleton of a young *E. maximus* bull (A.1225) at Manchester Museum was rigorously restored bone by bone, giving a shoulder height in the flesh of 253 cm (Appendix 1: S). Kurt and Kumarasinghe (1998) found that the average weight for a 257 cm bull in one of the studied populations was 3.2 tonnes, and according to Sukumar et al. (1988), a weight of 3.3 tonnes corresponds to a bull of 258 cm at the shoulders. The model produced a mass of 3.1 tonnes which corresponds perfectly with a healthy animal of the same shoulder height in good condition. The restoration of the famous circus elephant Jumbo (AMNH 3283) produced a mass of 6.1 tonnes at a shoulder height of 323 cm (Appendix 1: R); this body weight is expected for a bull of the same height in good condition (Laws and Parker 1968; Hanks 1972; see below). For comparison, the greatest

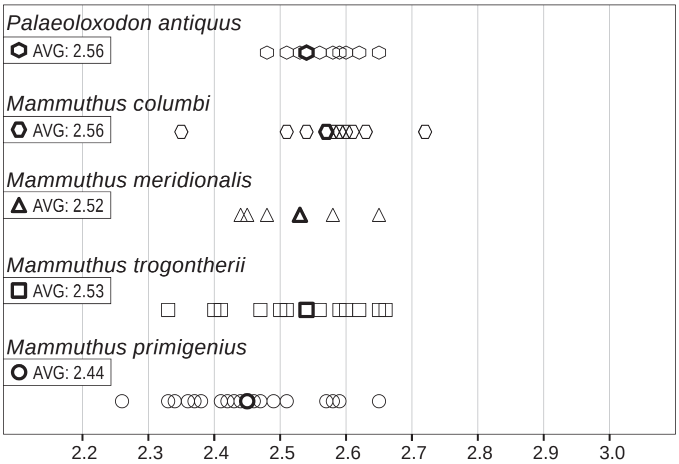

Fig. 6. Femur length vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data).

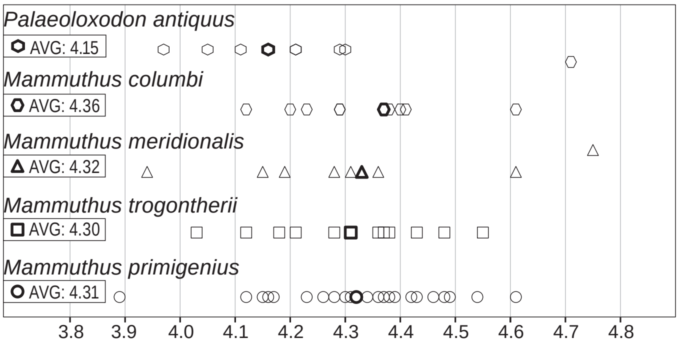

Fig. 7. Tibia length vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data).

body mass recorded for an African elephant is 6.64 tonnes, for an enormous wild bull near Ngaruka (Wood 1982). The front foot circumference measured 152 cm (Wood 1982), indicating a shoulder height of 334 cm. Another bull named Tembo recorded a weight of 6.25 tonnes on a controlled weighbridge a few months before his death, although it must be noted that there is no information about the nutritional condition of the animal. The animal had to lower his head when passing through his stall, which was 334 cm in height (Wood 1982), indicating a shoulder height very close to 330 cm.

Bone-by-bone skeletal reconstruction could be superior to a 3D scanned skeleton model, because usually there are important errors in the bone placement in extinct animal mounted skeletons. Proboscidean skeletons, even extant ones, are generally incorrectly mounted. There is often too much space between bones (limb bone elements and vertebrae), making the skeletons taller and longer, the anterior part of the chests are usually too wide and the posterior part of the thoraces are often too narrow because the posterior ribs are placed pointing downwards while in living elephants they go out almost horizontally, etc.

It is not possible to assign a simple plus or minus margin of error from an accurately restored model (Paul 1997). But the highly precise results obtained from the tested extant elephants and the resemblance of the skeleton of most of the extinct forms to those of living elephants, allow to assign a margin as low as ±10% when the skeletal restoration is complete enough. When there are not enough skeletal remains for an accurate restoration, the margin of error is probably about ±20%.

If a member (generally a species) of a group is restored, then it could be used as a guide for other members of the group, so further restorations for all could be redundant. The body mass obtained from a model represents only one individual, and body mass can vary considerably within species, so extrapolating masses between individuals should be done with care (see Paul 1997). There are some skeletal elements that carry clues for estimating the body mass of different individuals. The humerus length is the best indication to find out the shoulder height and therefore the body mass. Femur length is also closely related to the body mass and can be used as a reference. Pelvis breadth indicates the body bulk; in proboscideans the belly is generally equal to or barely wider than the hip region. The vertebral column's vertebrae corpus thickness is also important for estimating the articulated trunk length and overall size of the animal. The combination of these dimensions enables estimation of the mass of other species, genera or close groups from the already restored animals. The body masses listed in SOM: table 2, have been calculated on this basis.

The final point is that extant elephant body masses can vary by up to 10% within a year, depending on daily cycles of feeding, drinking and defecating, and on seasonal and reproductive cycles such as musth and pregnancy (Lister and Stuart 2010; Larramendi 2014). This is in accordance with the assigned error margins above.

Volumetric vs. allometric.—The results obtained from the volumetric method differ greatly from allometric formulae (Table 4), and these differences could have been even greater if equations with a percentage prediction error (PE%) over 15 had not been excluded from SOM: table 1. A comparison of the masses obtained from different proboscideans reveals that in most cases the discrepancies between the two methods are significant. For example, the body mass for Scoppito *Mammuthus meridionalis* obtained by the allometric method goes from 10.5 to 17.1 tonnes or up to 60% more than that obtained by GDI (10.7 tonnes). A body mass of 17 tonnes is too excessive for the Scoppito skeleton's volume and cannot be correct, the upper limit for this animal may be around 11.5–12 tonnes, even the obtained average body weight of 13.2 tonnes is still too high. The average body mass obtained for Zhalainuoer III *M. trogontherii* by two methods is quite similar, but the body masses obtained by allometric method for the other large bull 396 cm-tall *M. trogontherii* specimen (Azov I), are not reliable. An African elephant of this shoulder height is predicted to weigh about 10.5 tonnes, but the humerus and ulna dimensions of this mammoth produce body masses of around 14–17 tonnes, respectively, and an averge body mass of 12.7 tonnes (Table 4, SOM: table 1). These estimates are far from possible because the great resemblance between two genera's skeleton proportions at the same shoulder height. On the other hand, the body mass obtained by the volumetric method is only 10% more than predicted for a *Loxodonta africana* of its shoulder height, and the little difference in body mass can be explained because of the relatively wider pelvis of the mammoth. The similarity in the size of the bodies of the elephant and the mammoth confirms the accuracy of this result by GDI. Moreover, the very low body mass obtained by the allometric method for the Kolarik Mastodon (*Mammut americanum*), just 4.8 tonnes, is an astounding result and hardly credible considering that this weight corresponds to a slender-proportioned *L. africana* barely less than 3 metres tall and that the volume of the 269 cm-high mastodon is about 35% more. The less accurate results of allometric estimates show important body mass/bone dimension differences between extant and extinct forms. So, the allometric method is not accurate enough for calculating the body mass of extinct proboscideans. Finally as shown above, the body masses obtained by allometric formulae for extant forms are not realistic. However, the results obtained by volumetric calculations correspond perfectly with living elephants (SOM: table 1).

Biological implications of body size and biomechanics

Age determination.—The best way to estimate an extinct proboscidean's ontogenetic age is to compare the stage of tooth eruption and wear with the analogous data that Laws (1966) compiled for a set of mandibles of African elephants (*Loxodonta africana*). His results were revised by Jachmann (1988). The large body size of many extinct proboscideans implies a longer lifespan than that of African elephants. Blueweiss et al. (1978) created a formula where the longevity in days is proportional to body mass in grams$^{0.17}$. The average body masses of larger extinct forms were found out first (see Appendix 1, SOM: table 2) and a longevity of 60 years and a body mass of 6 tonnes for *L. africana* are assumed. So, using Blueweiss et al. (1978) and assuming the above parameters, the longevity of extinct forms was calculated (Table 5). The ages shown in SOM: table 2 and the Appendix 1 were calculated on the basis of the stages of wear of the teeth and the lifespan obtained for different species.

The lifespan of the largest extinct species such as *Mammut borsoni* and *Palaeoloxodon antiquus* might be about 10 years or more more than extant elephants according to Blueweiss et al. (1978) allometric formula, but the results should be taken with caution, because these figures could be somewhat conservative given that the complete fusion of long bone epiphysis in some giant proboscideans might occur as late as 50 regardless of sex (Larramendi 2014), which is 25% later than extant elephants in the case of males and twice that in the case of females. So a longevity of 75 years or considerably more is therefore equally possible in giant extinct proboscideans.

Hair and skin surface area.—Hair has an important effect on thermoregulation in elephants. In fact, there is usually a significant negative correlation between hair density and body size in mammals. However, some extinct proboscideans had an extremally high hair density despite their large size. The cold-adapted *Mammuthus primigenius* was entirely covered with a thick coat of hair and had a very short tail as would be expected. The American mastodon might have been covered with hair because of the seasonally cold climate, although there are few soft tissues preserved that could help to support this idea. The only reliable hairs attributable to *Mammut americanum* were recovered in association with cranial fragments near Milwaukee (Haynes 1991). The reported hairs during the nineteenth century were in fact green algae filaments (Eisley 1945). Finally, the relatively long tail (up to 27 caudals; Haynes 1991) and the massive body of *M. americanum* suggest that the prevalent ideas that these animals were covered with a thick coat of fur are probably exaggerated. On the other hand, there are the gomphotheres, an extremely successful group that lived from the Late Oligocene to the Pleistocene (Kappelman et al. 2003; Alberdi et al. 2007; Wang et al. 2013). The particular case of the genus *Gomphotherium* is exceptional. It lived for over 20 million years and was widespread throughout Africa, Eurasia, and North America, and was able to survive many glaciations (see glacial periods; Böse 2012; Rutter et al. 2012). Some species within this genus had very short tails, *G. steinheimense* had only 20 caudal vertebrae, which produced a very short tail (Göhlich 1998; Appendix 1: M); in comparison, *M. primigenius* presented 21 caudals (Osborn 1942; Larramendi 2014). The DMNH 1261 *G. productum* skeleton had only four caudal vertebrae preserved, but judging by their small size, the entire tail of this individual had to be very short too (Appendix 1: L). The fact that some *Gomphotheirum* species could have lived in cold conditions and the very short tail presented in this genus, suggest that several species were probably covered

Table 5. Estimation of lifespan (in years) of different proboscidean species based on the calculated average body mass (in tonnes), after Blueweiss et al.'s (1978) formula.

Species	Average body mass	Estimated life span
Mammuhtus primigenius	6	60
Mammuthus columbi	9.5	65
Mammuthus trogontherii	11	67
Mammuthus meridionalis	11	67
Mammut americanum	8	63
Mammut borsoni	16	71
Deinotherium proavum	10.5	66
Palaeoloxodon antiquus	13	68

with a thick coat of hair and therefore other members of the Gomphotheriidae family may have been covered with hair as well. Most archaic members of Proboscidea (*Eritherium*, Moeritheriidae, Numidotheriidae, and Barytheriidae) were probably covered with hair because of their low body volume to skin surface ratio. The hair would have been very helpful in maintaining body temperature in the small forms. In most mammals the relationship between body size and hair density represents a thermoregulatory adaptation because larger animals have increased difficulty dissipating heat due to the scaling of surface area to volume (Schwartz and Rosenblum 1981). Because of the heat transfer problem of big land mammals, they have low hair density. The largest animal today that is entirely covered with a dense hair is the giraffe, *Giraffa camelopardalis*. The largest bulls attain a body mass of about 1.2–1.5 tonnes (Wood 1982; Skinner and Smithers 1990; Mitchell and Skinner 2009), while land mammals over this weight, Hippopotamidae, Rhinocerotidae, and Elephantidae, are not covered with a high density of hair, although it is worth noting that extant elephant hair is the first documented example in nature where sparse hair increases the effective heat transfer coefficient, and this therefore raises the possibility of such a covering for similarly sized proboscideans in the past (Myhrvold et al. 2012).

Despite the very high body volume to skin surface ratio, *M. primigenius* was totally covered with a thick coat of fur. This hair helped mammoths to endure extreme cold temperatures and the heat loss after they drank chilled water (Haynes 1991). Larramendi (2014) calculated that the average fresh hair weight over the body of the North Siberian *M. primigenius* would have been 4 kg/m^2 on the basis of a comparative analysis with the extant muskox, *Ovibos moschatus*. It should be noted that the amount of hair would have varied over a year, depending on seasonal changes and other factors. So the estimated hair mass should be taken as approximate only. The larger European forms, weighing on average 1/3 more than most northern latitude specimens (Table 8), probably had less and shorter hair, so 3 kg/m^2 is more reasonable for the European populations. The 3 kg/m^2 proposed by Larramendi (2014) for the cold-adapted *M. trogontherii* is excessive because of the enormous size of this species; 2 kg/m^2 or less would be more reasonable. The insufficient information on mastodonts, archaic proboscideans and other mammoths, makes impossible to estimate for them the average hair weight per square metre.

To calculate how much the entire coat could have weighed in woolly and steppe mammoths, first the total body surface was calculated. In isometric objects, the surface areas are proportional to the volume$^{2/3}$ and can be estimated from the masses (Kleiber 1961), but as animals grow allometrically and important skin surface variations appear to be on elephants with a similar body mass (Table 6), the approximate total lateral surface area (exluding the soles) of each studied specimen was calculated as per Hurlburt (1999) and Larramendi (2014), who calculated the curved surface area as an elliptical cylinder summing the approximate elliptical perimeters (P) of the obtained cross sections (each one of 1 pixel in length) from the studied specimens and applying the following formula:

$$P = 2\pi \sqrt{(0.5)(r_1^2 + r_2^2)}$$

where P, perimeter; r, radius.

The results were compared with the measured surfaces of 24 Asian elephants irrespective of sex by Sreekumar and Nirmalan (1990). The average body mass of the specimens studied by Sreekumar and Nirmalan (1990) was nearly 3 tonnes with a mean skin surface of 17.2 m^2. The estimated total skin surface for A.1225 *Elephas maximus* in this study is 16.8 m^2 with a body mass of 3.1 tonnes, a result within the range of an animal of its weight. Therefore the results obtained for extinct forms are reasonably reliable (Table 6). The calculated skin surface area for the Siberian Taymir mammoth is 18.5 m^2, and approximately 74 kg of hair is therefore predicted, while the much larger Siegsdorf woolly mammoth has a total skin surface of 31 m^2, and therefore about 93 kg is predicted in this case. The Warren mastodon (AMNH 9950), with a nearly identical body mass to the Siegsdorf mammoth, has 4 m^2 less body surface due to the more rounded body of the mastodon. Finally, the Zhalainoer III *M. trogontherii* is predicted to have about 75 kg of hair, 35 kg less than was calculated by Larramendi (2014). The 88 m^2 of skin surface for a large African elephant calculated by Myhrvold et al. (2012) is definitely excessive; in comparison, Gunga et al. (2008) calculated the total skin surface of the gigantic *Giraffatitan brancai* sauropod dinosaur to be 119.1 m^2 with a body vol-

Table 6. Estimation of skin surface of different proboscideans, including extinct forms, that might have carried a thick layer of hair.

Species	Individual	Body mass without hair (tonnes)	Skin surface area (m^2)	Reference
Mammut americanum	AMNH 9950	7.8	27	this paper
Mammuthus trogontherii	Zhalainuoer III	10.3	37.3	this paper
Mammuthus primigenius	Siegsdorf	8.1	31	this paper
Mammuthus primigenius	Taymir	3.8	18.5	this paper
Elephas maximus	A.1225	3.1	16.8	this paper
Elephas maximus	sample of 24 individuals	3	17.2	Sreekumar and Nirmalan 1990
Elephas maximus	Iki	2.2	12–13.3	Shoshani et al. 1982
Gomphotherium productum	DMNH 1261	4.6	19.1	this paper
Gomphotherium steinheimense	Mühldorf	6.7	25.6	this paper

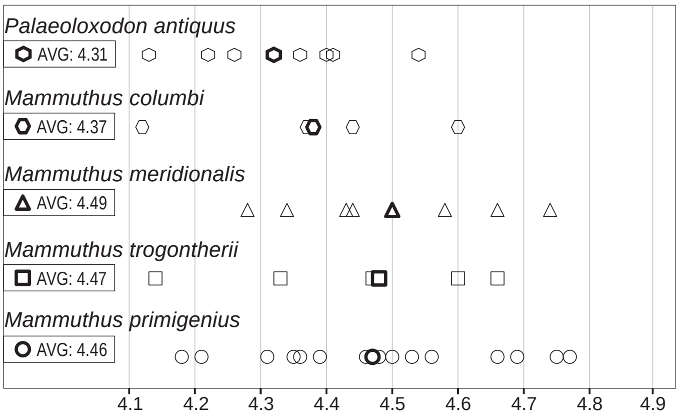

Fig. 8. Fibula length vs. skeletal shoulder height ratio of selected proboscideans based on the data collected in this study (Appendix 1, SOM: table 2; AL unpublished data).

ume of 47.9 m^3 or six times the body volume of a fully grown *Loxodonta africana*. The problem is that Myhrvold et al. (2012) assumed a body 6 m-long and 3 metres in diameter and treated it as a circular cylinder; in fact, these dimensions are more than twice the real body measurements of a very large *L. africana*. The calculated skin for a large Jumbo (AMNH 3283) elephant is 29 m^2 (including the enormous ears) or 1/3 that calculated by Myhrvold et al. (2012) for a large African elephant. Thus the heat flux density to release all the metabolic heat generation would be three times more than that proposed by Myhrvold et al. (2012).

Locomotion.—Extant elephants and sloths are the only land mammals unable to run with a suspended phase in the stride (Gambaryan 1974; Paul 1998; Hutchinson et al. 2003; Christiansen 2007). Fast-running animals have flexed elbows and/or knees, relatively long tibia in relation to the femur, and long manus and/or pedi elements that act as active springs to increase the propulsive effect of the legs (Gambaryan 1974; McMahon and Bonner 1983; Paul 1987, 1998). Thus, it has been suggested that elephants' inability to run is due to their pillarlike limbs (Gambaryan 1974; Haynes 1991; Paul 1998; Paul and Christiansen 2000). However, a recent study (Ren et al. 2008) concluded that elephant limbs are significantly less columnar than previously thought and that the joint ranges of motion are similar to those of horses at comparable speeds. Nevertheless, Ren et al. (2008) did not report scapula and pelvis angles, and using markers on the skin may lead to considerable errors (Günther et al. 2003; Paul 2009). First, it has to be said that it is not easy to compare horse and elephant bone dispositions due to the large differences in the relative lengths of the bones. For example, distal elements in elephants are extremely short and massive, unlike horses, all ungulates and running animals. This automatically places the wrist and ankle much higher in horses than in elephants, giving to horses full liberty to rotate metacarpals (anteriorly) and metatarsals (posteriorly), unlike elephants where those joints are much more rigid and do not freely move and are not able to rotate greatly posteriorly. In a standing horse the degree of shoulder angle, between the humerus and along the axis of the scapula, is nearly 90º (see Goldfinger 2004; Frandson et al. 2009), whereas in elephants there is a nearly straight angle at around 170º, making this segment nearly columnar in elephants and very flexed in horses. In trotting horses and in ambling elephants, this segment is still expected to be considerably more flexed in horses because the scapular rotation is lower in elephants due to its longer limbs (Fischer and Blickhan 2006). Furthermore, the angle between the ulna and humerus is also considerably more pronounced in a horse than in an elephant due to the more inclined humerus of the horse. Finally, the angle between the pelvis and femur is also more obtuse in horses than in elephants, this angle approaches a right angle in horses and in the case of elephants it is nearer to a straight angle (see Goldfinger 2004; Frandson et al. 2009). Therefore, although some limb segments of elephants could be as flexible as horses at comparable speeds, unlike what was previously thought (Ren et al. 2008), other appendicular element dispositions indicate that elephants are still considerably more columnar than horses and other running animals.

The inability of elephants and practically all proboscideans to perform true running with a suspended phase may be due to a combination of different factors or features: (i) the diaphysis of the femur and other long bones is larger in lateromedial than anteroposterior diameters (Christiansen 2007); (ii) the cnemial crest of the tibia is relatively poorly developed, indicating that the muscles attached there are not as strong as in other running animals such as rhinos and horses (Haynes 1991); (iii) the ilium is realtively short and therefore not suitable for big muscle attachments (Paul 1998), indicating a low ratio between limb muscle mass and total body mass (Taylor et al. 1974; Weibel et al. 1987); (iv) the proximal segments of the appendicular skeleton (scapula/humerus humerus/ulna and pelvis/femur) are poorly flexed; (v) the relatively long humerus and femur, short tibia and the composition of the manus and pedi with very short and relatively rigid distal elements (especially metacarpals and metatarsals) and big pads are not suitable for a strong propulsive phase of the limb stroke. All these characteristics are highly divergent from those of most running mammals and birds (Paul 1998, 2009; Christiansen and Paul 2000; Christiansen 2007) and have more influence than the high body mass of elephants because calf and juvenile individuals are also unable to perform true running. Some of these characteristics were not present in the earliest proboscideans such as *Moeritherium* (see Andrews 1906; Christiansen 2007; Appendix 1: A). Extant elephants' rare mode of locomotion probably began to dominate in Plesielephantiformes onwards (see Christiansen 2007). It is likely that the earliest members, including *Eritherium*, *Moeritherium* and probably some Plesielephantiformes, were able to run with a suspended phase in their stride due to the differences in the appendicular skeleton, including more flexed limbs. The very long-bodied *Moeritherium* was probably able to trot but not gallop, similar to modern hippos, and therefore probably wouldn't have reached high speeds. The fastest and most reliable speed recorded for an elephant is 6.8 m s^{-1} (25 km h^{-1}) (Hutchinson et al. 2003) measured on an athletic young bull (~2.8 tonnes) Asian elephant (Hutchinson et al. 2006). Past estimates claiming speeds up to 40 km h^{-1} are dubious (Andrews 1937; Bakker 1975; Garland 1983). Larger extant and extinct proboscideans are/were probably not able to reach or surpass significantly the maximum recorded speed (although there might be some exceptions) because joint angular velocities decrease notably with increasing size (Ren et al. 2008). The stronger limb bones of mastodonts do not necessarily indicate faster locomotion; this has more to do with their relatively higher body mass. The barely more flexed limbs might give them the possibility of developing slightly higher speeds, but there is not enough evidence to imply a significally different locomotor mechanism from that of extant elephants. Some features of deinotheres may suggest a faster or at least more agile locomotion than living elephants, they had a short humerus (generally about the same length as the ulna), relatively high capacity to flex the ulna, considerably elongated tibia and very long metacarpals and metatarsals, unlike other members of Proboscidea. Furthermore, in *Deinotherium*, the scapular spine lacks the acromion and a metacromion (Harris 1978). The muscles attached in the metacromion are involved with scapular stabilization and humeral rotation (Salton and Sargis 2008) and the absence of these processes appears to be a cursorial modification in artiodactyls (Smith and Savage 1956); thus, this feature in deinotheres gave more mobility to the scapula and humerus, enabling an extra boost during ambling and additional mobility in the proximal segment, helping the animal to reach the ground due to the predicted relatively short proboscis.

Some palaeoloxodont and mammoth species such as *Palaeoloxodon falconeri*, *P. tilensis*, *P. mnaidriensis*, and *Mammuthus lamarmorai* show a particular feature on forelimbs, the presence of fused zeugopodials (ulna and radius) (Amborsetti 1968; Ferreti 2008; Palombo et al. 2012). This probably indicates a locomotory adaptation due to a more strenuous locomotor activity as they might have had to move on more arduous terrain or they ambled proportionally faster, but it is unlikely that they were able to run with a suspended phase in their stride because they had similar appendicular skeleton proportions to extant elephants.

Extant elephants' size

Today three species of elephants are recognized, the African forest elephant, *Loxodonta cyclotis*, the African bush elephant, *Loxodonta africana* and the Asian elephant, *Elephas maximus*. Body size differs greatly among the fully-grown extant proboscideans. The complete fusion of long-bone epiphyses in today's elephants occurs late among males, around the age of 40, and at around the age of 25 in females (Roth 1984; Haynes 1991; Lister 1999; Larramendi 2014). It is thus expected that elephants attain their maximum stature by the end of the long-bone epiphyseal fusion. Both sexes, however, seem to continue growing throughout their lives (see Laws 1966; Lindeque and van Jaarsveld 1993). For this paper, fully-grown individuals are considered to be those who have completed their long-bone epiphyseal fusion.

The average shoulder height of a fully-grown *Loxodonta cyclotis* is much less than that of African bush elephants. Not many studies have paid particular attention to the size of this species, but most of them give a shoulder height of only about 2 metres (Morrison-Scott 1948; Wood 1982). In good conditions this could reach 220 cm at the shoulders (see Morgan and Lee 2003). By contrast, the African bush elephant, *L. africana*, is much larger and is the biggest land mammal today. Many studies have examined different populations' shoulder heights, and it can be stated that the average shoulder height in good conditions for this species is 260 cm for females and 320 cm for males (see Laws 1966; Laws and Parker 1968; Short 1969; Hanks 1972; Laws et al. 1975; Lang 1980; Wood 1982; Haynes 1991; Lindeque and van Jaarsveld 1993; Lee and Moss 1995; Shrader et al. 2006; Della Rocca 2007). Finally, the average shoulder height in good conditions for *E. maximus,* according to several researchers, can be set at 240 cm for females and 275 cm for males (Wood 1982; Sukumar et al. 1988; Kurt and Kumarasinghe 1998).

Strong sexual dimorphism in body size is observed among extant elephants, which is considerably more remarkable in *L. africana* than in *E. maximus*. African bush male elephants are on average 23% taller than females, and Asian elephant males are only about 15% taller than females.

In terms of weight, it is well known that there is a very close relationship between shoulder height and body mass among extant elephants (Johnson and Buss 1965; Hanks 1972; Laws et al. 1975; Roth 1990; Christiansen 2004). Many different formulae have been developed to estimate elephant body masses based on shoulder heights, with a very high correlation coefficient (Johnson and Buss 1965; Hanks 1972; Laws et al. 1975; Roth 1990; Christiansen 2004). An equation frequently used to estimate the body masses of male *Loxodonta africana* elephants, developed by Laws et al. (1975) based on Murchison Falls Park South elephants (M.F.P.S.), is as follows:

$$BM = 5.07 \times 10^{-4} \times SH^{2.803}$$

where BM is body mass in kg and SH is shoulder height in centimetres. There is, however, a problem with the formula because it gives underestimated results. This is due to the fact that the measured population (M.F.P.S.) was well below the optimal physical condition for the species, despite the sample being collected in a favourable season of the year (Laws et al. 1975). At 300 cm, the weight of M.F.P.S. elephants was on average 4450 kg, which is 11% less than Mkomasi elephants (5000 kg) of the same shoulder height (Laws et al. 1975). The best weight-height relationship was shown by the Mkomasi elephants sample (Laws et al. 1975). Thus, the body mass of an average-sized African male bush elephant at 320 cm in good condition is expected to be around 6000 kg, a weight already observed in different elephant populations with the same shoulder height (Laws and Parker 1968; Hanks 1972). Based on published body masses from different populations of female *L. africana* (Laws and Paker 1968; Hanks 1972; Laws et al 1975), at 260 cm shoulder height a body mass of 3000 kg (non-pregnant) is expected in good conditions. However, the published equations by Laws et al. (1975) give slightly lower results at this shoulder height by ~5%; in contrast, the equations published by Hanks (1972) and Roth (1990) give a 10% higher body mass than expected. No study has focused on the body mass of *L. cyclotis*, but an average African forest elephant male of 220 cm at the shoulders should be around 2000 kg as its body shape is very similar to that of *L. africana*.

There is a strong belief that Asian elephants are much heavier than African elephants of the same shoulder height (Roth 1990; Christiansen 2004; Lister and Stuart 2010). This concept has developed because the body mass data obtained for *E. maximus* has generally been taken from captive individuals (zoo and circus animals). Comparing the weights obtained from *E. maximus* by several authors (Benedict 1936; Wood 1981; Christiansen 2004) with the data from wild and captive animals under optimal nutritional conditions (Sukumar et al. 1988; Kurt and Kumarasinghe 1998), it can be stated that the generally used data came from clearly obese animals, some specimens from Benedict (1936) and Christiansen (2004) are up to 60–85% heavier than elephants of the same shoulder height in good conditions (see Kurt and Kumarasinghe 1998). An average-sized male *E. maximus* (275 cm), in optimal conditions, is about 4000 kg and an average fully grown female elephant (non-pregnant) is around 2700 kg (Sukumar et al. 1988; Kurt and Kumarasinghe 1998). The fact is that *E. maximus* is only slightly heavier than *L. africana*. It is true that *E. maximus* has a proportionally broader pelvis and more compact body than the African elephant, but *L. africana* has a more elongated body. This means that there are no significant differences in body mass between *E. maximus* and *L. africana* of the same shoulder height. These differences are mainly due to the fact that it is not possible to compare both species in the same conditions. A 275 cm male *E. maximus* is a fully grown individual, while a male *L. africana* of this shoulder height is a sub-adult animal and is not as robust as a fully mature individual (see Hanks 1972). Therefore the African elephant would be less heavy. But if we compare both species at 300 cm, both of them will attain nearly the same body mass of about 5000 kg, because the Asian elephant gets more slender at this shoulder height (due to allometry, see below) and the African elephant gets broader because it is nearly a fully-grown animal.

Based on different African male/female populations and mixed Asian elephants and using the body masses obtained for average-sized individuals in good condition of both extant species, several equations were developed for animals from calves to fully grown average-sized individuals (see Table 7). For male *L. africana*, the average growth rate (exponent) was found based on Laws (1966) and Laws et al. (1975) different male *L. africana* populations. The equation was tested on individuals measured under optimal conditions: Mkomasi elephants (Laws et al. 1975), data given by Laws and Parker (1968); a large wild elephant from Ngaruka (Wood 1982); Tembo elephant (Wood 1982); and Jumbo elephant (AMNH 3283), which has been calculated in this study. The results correspond closely with the body masses obtained in the mentioned samples with a very high correlation coefficient (0.999) and very low average percentage prediction error (%PE = 1.19). For female *L. africana*, the proposed equation was based on the average growth curve from female African elephants studied by Laws et al. (1975) and tested on elephants in optimal conditions described by Laws et al. (1975), with the information given by Laws and Parker (1968), Hanks (1972) and the NMNS002990-F002715 specimen, also calculated in this paper. For the females, the results also show a high correlation coefficient (0.963) and low average percentage prediction error (%PE = 4.55). For *E. maximus,* the developed equation was tested on Asian elephants of both sexes with the data given by Sukumar et al. (1988) and Kurt and Kumarasinghe (1998). The correlation coefficient (0.988) and the average percentage prediction (%PE = 3.18) were very low in this case too.

Consequently, average sizes have been calculated in this study for extinct forms in good conditions based on the body masses and shoulder heights in the flesh (Appendix 1, SOM: table 2). Equations for extinct forms (*Deinotherium proavum*, *Mammut borsoni*, *Mammut americanum*, *Palaeoloxodon antiquus*, *Mammuthus meridionalis*, *Mammuthus trogontherii*, *Mammuthus meridionalis*, *Mammuthus columbi*, and *Mammutuhus primigenius*), also based on the average growth curve of extant elephants of both genera (Laws et al. 1975; Roth 1990), were calculated. These equations, tested on the shoulder heights and body masses of a wide range of specimens, from young to average-sized individuals, yielded highly reliable results. A high correlation coefficient (r) was obtained, varying from 0.957 to 0.999, with a low average prediction error (%PE) ranging from 0.71 to 5.47 (Table 7).

All the published equations based on shoulder heights to estimate body masses of extant elephants are only valid up to average-sized specimens (see Roth 1990), and thus one wonders what occurs in expecially large individuals.

Exceptionally tall individuals and allometry.—Among modern animals there is a very small percentage of record-sized individuals. These specimens are extremely rare, usually there is one among hundreds of thousands, or even millions. With regard to modern elephants, record-sized specimens are about 25% taller than average. The tallest *Elephas maximus* on record was a huge male shot in Assam, India, in 1924. Using the conventional method of multiplying the forefoot circumference by two (Wood 1982;

Table 7. Developed equations for body mass estimation of different proboscidean taxa from young to average-sized individuals and from large (> 5% taller than average) to record-sized individuals, based on the relationship between shoulder height (SH) and body mass calculated in this study. Correlation coefficients (r) and prediction errors (PE) are not possible to calculate for specimens within Grade II to IV, because these equations are based on the proposed allometric growth curve (see Fig. 9) for animals above the average, and can not be tested because the scarcity of the individuals of this size range.

Species	Body mass equation	Size range	Gender	r	Average % PE
Loxodonta africana	$3.28 \times 10^{-4} \times SH^{2.899}$	young – Grade I	males	0.999	1.19
	$2.2 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
	$3.22 \times 10^{-4} \times SH^{2.886}$	young – Grade I	females	0.963	4.55
	$1.88 \times 10^{-4} \times SH^{2.569}$	Grade II – Grade IV	females	–	–
Elephas maximus	$3.21 \times 10^{-4} \times SH^{2.903}$	young – Grade I	mixed	0.988	3.18
	$2.165 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
	$2.07 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	females	–	–
Deinotherium proavum	$3.83 \times 10^{-4} \times SH^{2.903}$	young – Grade I	mixed	0.983	5.47
	$2.75 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	mixed	–	–
Mammut borsoni	$4.16 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.999	0.57
	$3.11 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
Mammut americanum	$5.69 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.972	2.69
	$3.78 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
Palaeoloxodon antiquus	$3.63 \times 10^{-4} \times SH^{2.903}$	young – Grade I	mixed	0.993	3.01
	$2.69 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	mixed	–	–
Mammuthus meridionalis	$3.08 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.979	2.15
	$2.2274 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
Mammuthus trogontherii	$3.08 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.971	3.94
	$2.2274 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
Mammuthus columbi	$3.2 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.958	3.24
	$2.2322 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
Mammuthus primigenius (European form)	$3.36 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.962	3.82
	$2.2293 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–
Mammuthus primigenius (North Siberian form)	$3.54 \times 10^{-4} \times SH^{2.903}$	young – Grade I	males	0.957	1.16
	$2.2327 \times 10^{-3} \times SH^{2.569}$	Grade II – Grade IV	males	–	–

Sukumar et al. 1988), it was estimated to be 343 cm at the shoulders (Pillai 1941; Wood 1982). A few more individuals of this size category have been reported in recent history (Wood 1982; Lister and Blashford-Snell 1999). On the other hand, the tallest *Loxodonta africana* bulls on record probably reached 400 cm at the shoulders (Wood 1982). The largest, accurately-measured African bush elephant was a gigantic bull shot in Angola in 1974 (Ward et al. 1975; Wood 1982; Haynes 1991). Its forefoot circumference was measured at 180 cm (Wood 1982), indicating a shoulder height of 396 cm. The shoulder height of mature *L. africana* can be calculated by multiplying the circumference of the forefoot by 2, plus 10% (Wood 1982). The projected line from the highest point of the scapula of this individual to the base of the extended forefoot, whilst lying on its side, was measured at 417 cm, again indicating a shoulder height of about 396 cm. There is a difference of about 5% between the standing and lying shoulder height of extant elephants because the great weight tends to spread the body out laterally (Shoshani et al. 1982 contra Hanks 1972; Wood 1982). However, important calculation errors could have been made in several record-sized specimens. In November 1955 an enormous elephant (popularly known as Fenykovi) was shot in the same area. This one was measured at 401 cm on its side, suggesting its size to be 381 cm at the shoulders (Wood 1982). This specimen is stored at the Smithsonian Natural History Museum and catalogued as USNM 304615. The postcranial long-bone diaphyseal lengths of this specimen (Roth 1990) show an animal nearly 10% taller than Jumbo (AMNH 3283), indicating a shoulder height in the flesh of about 350 cm and 7.5 tonnes of body mass, very far from previous estimates of 31 cm (381 cm) in shoulder height and nearly 3.5 tonnes (10.9 tonnes) in body mass (Wood 1982).

The biggest African elephants on record are usually estimated to be up to 12 tonnes of body mass (Wood 1982; Paul 1997). These estimates correspond to an isometric growth, but land animals change their proportions as they grow and tend to become more robust and massive as they become bigger. This is true for most land mammals. Mature elephants attain greater body mass than sub-adult individuals of the same shoulder height (see Kurt and Kumarasinghe 1998), and in African elephants over 30 years of age the height increases much less than the weight (Hanks 1972). Therefore, proboscideans tend to become stockier as they mature (there can be exceptions to this rule depending on nutritional conditions and other factors). Does this mean that exceptionally tall bulls are proportionally heavier? Or, at least, relatively as heavy as fully grown average-sized specimens? Probably not. It is known that in Namibia, where exceptionally tall elephants survive, they have relatively longer legs (Wood 1982), indicating a negative body mass allometry in unusually tall elephants; they are relatively less heavy compared

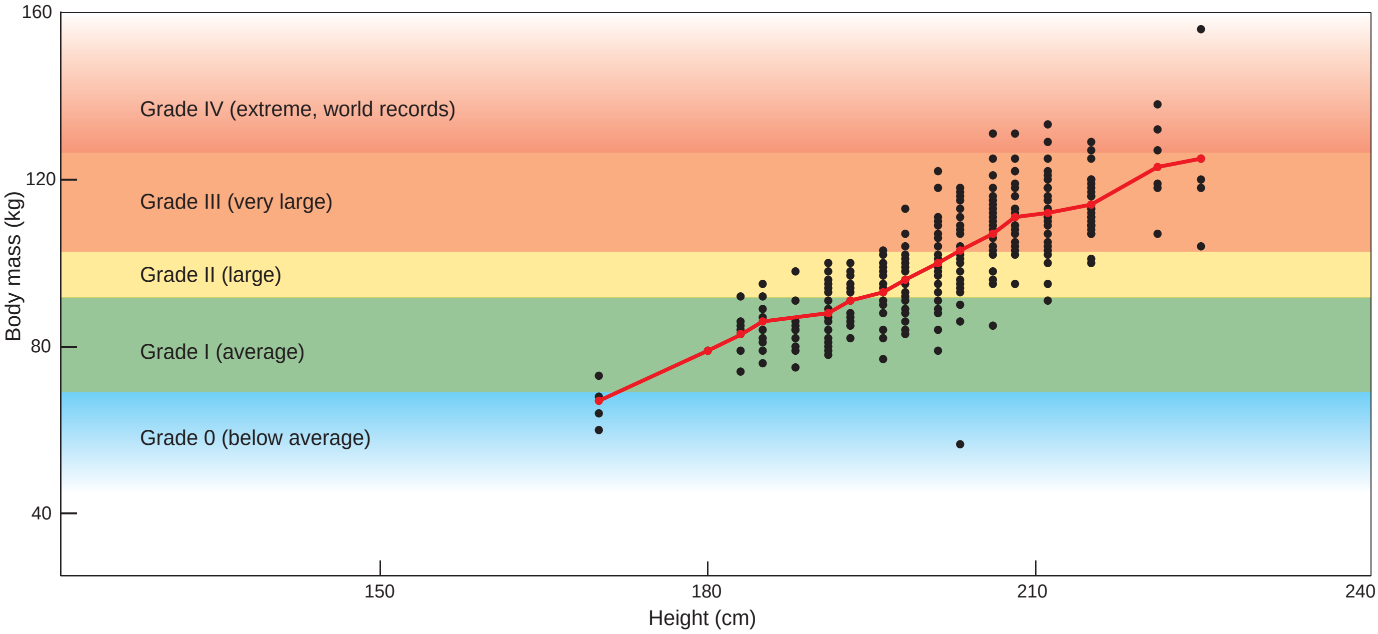

Fig. 9. Plot of height vs. weight for 561 male *Homo sapiens* in optimal conditions from 170 cm (low average) to 225 cm tall. Average growth curve (red line).

to the shoulder height as they have longer legs, and therefore relatively shorter and narrower bodies. Therefore, a strong negative allometry is also expected for oversized elephants. Gould (1966) also observed an intraspecific mandible size decrease vs. body length in *Lucanus mearesi,* in specimens above average. It is also known that larger animals have a general tendency toward shorter torso relative to the width and head length vs. body length relationships, which almost always show negative allometry due to the relatively decreasing brain size (Gould 1966). These same results can be observed in very tall humans, where a relatively long arm and leg length vs. torso length is a rule, as is a relatively small head size. This is due to the decreasing brain weight/body size relation.

To date, no study has extensively dealt with allometry in above-average-sized animals; all studies, especially those focused on elephants, have created allometric formulae based on calf to fully grown averaged-sized mature individuals (Johnson and Buss 1965; Hanks 1972; Laws et al. 1975; Roth 1990; Christiansen 2004). The main problem is the scarcity of individual animals much larger than the average ones, so it is extremely difficult to find a growth curve from average-sized wild animals to world record specimens. However, for this work, the data of the only animal with vast data on this subject was used, *Homo sapiens*. The average height of today's male humans in good conditions is about 180 cm (Ogden et al. 2004; Garcia and Quintana-Domeque 2007; Hatton and Bray 2010). The tallest healthy humans in the world can reach statures 25–30% taller than the average, and even taller humans have been reported, but these individuals generally suffer from a pathology such as gigantism.

The selected sample is a homogeneous group of athletes (561 individuals) with optimal nutritional and physical conditions, parameters also present in wild animals in good condition. The average body mass at a height of 180 cm was found to be 79 kg. Assuming isometry, individuals 25% taller than average will be 95% heavier or 154 kg, but the reality shows that at 225 cm the average body mass of *Homo sapiens* in optimal conditions is 125 kg or 58% more than average and 19% less than expected (Fig. 9), indicating a strong negative allometry in individuals that are much taller than average.

With regard to the two equations for male individuals developed by Laws et al. (1975) for the estimation of mass from shoulder height, at 400 cm or 25% more than average, body masses are 87% and 91% more than average, indicating nearly an isometric growth for record-sized individuals. The body masses obtained for record-sized individuals applying the equations developed by Roth (1990) for *Elephas maximus* mixed populations are up to 107% more than average, indicating a positive allometry in this case. Therefore all these equations overestimate the body masses of above-average-sized individuals and aren't good for estimating the body masses of particularly big elephants. It is probably too excessive to apply the *Homo sapiens* growth curve to elephants above the average, because humans are bipeds so the weight is held only on two supporting points compared to the four of elephants. Thus exceptionally tall elephants could distribute the body weight better than humans, and therefore lighter negative allometry is expected for elephant body masses above average. For this study an intermediate negative allometry growth curve is proposed (Fig. 10), so the body mass for record-sized elephants (25% taller than average) is expected to be around 77% more than average. Therefore, the tallest *Loxodonta africana* on record (396 cm) is predicted to have weighed 10.4 tonnes, 1.9 tonnes less than previous estimates (Wood 1982). Meanwhile the tallest *E. maximus* (343 cm) is estimated to have had around

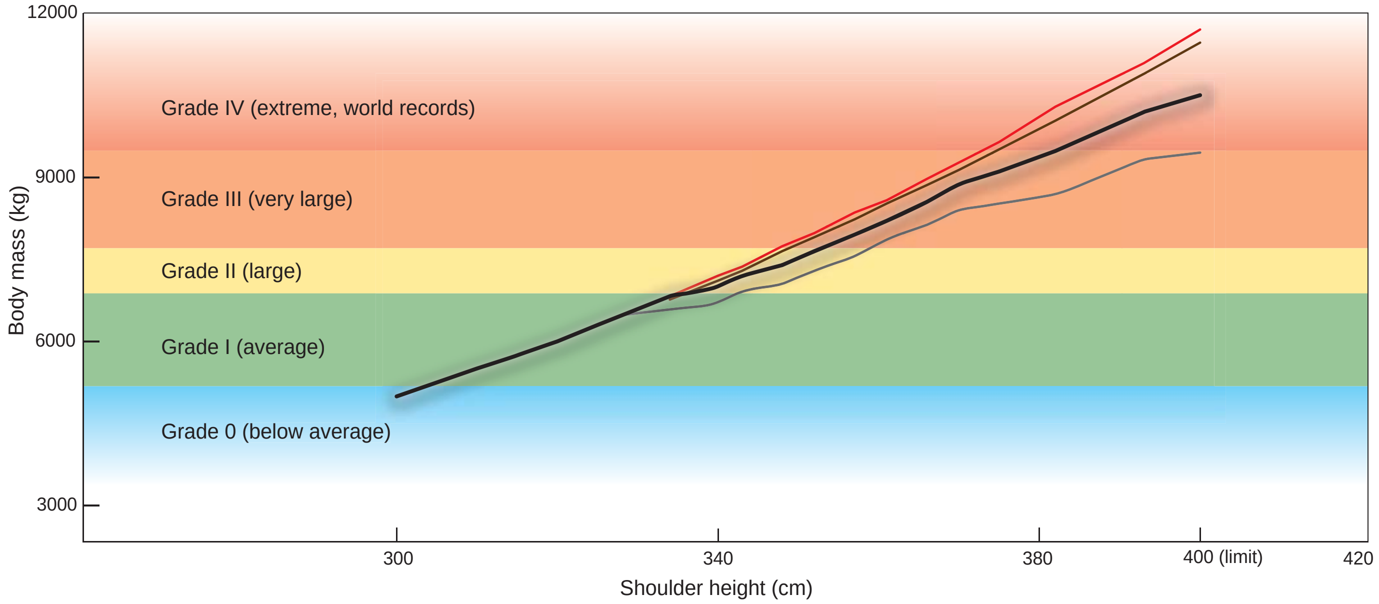

Fig. 10. Different growth curves for *Loxodonta africana* from average-sized to world record specimens based on isometric growth (red), Laws' (1975) equations for wild population in good conditions up to average size (brown), *Homo sapiens* (in optimal conditions) allometric growth (grey), and the proposed allometric growth curve for proboscideans in this study (black).

7 tonnes of body mass. Using the obtained growth curve, different equations for extant and several extinct proboscideans have been developed (Table 7).

Around 90% of the shoulder heights of fully grown individuals observed from any population of modern elephants fall into a size range ±5% of the average height of the population (see Laws et al. 1975; Kurt and Kumarasinghe 1998). The rest are below or above the average in similar proportions. Five size classes are proposed to sort out and find the size limit of extant and extinct proboscideans (Table 8): Grade 0 (small): Represents about 5% of the population. This size class represents individuals under the average size. Grade I (average): Represents about 90% of the population. The size range (shoulder height) is ±5% of the average height found in good conditions for each species. Grade II (large): Represents about 5% of the population. The size range is 5–10% taller and 11.5–28% heavier than average. Grade III (very large): Represents only about 0.1% of the population. The size range is > 10–20% taller and > 28–59% heavier than average. Grade IV (world record specimens): The presence of individuals in this size class is extremely rare, probably less than 0.001% of the population. The height range is > 20–25% taller and 60–77% heavier than average.

Extinct proboscideans size

Early proboscideans.—The first proboscideans, which evolved and diversified in Africa during the Paleogene, were very small. *Eritherium azzouzorum* is the earliest recognized proboscidean from the middle Paleocene (60 Ma) of Morocco (Gheerbrant 2009). The holotype (MNHN PM69) is an anterior part of the skull with maxilla and zygomatic arches. Judging by the extremely small size of the preserved material, and assuming a sirenian-type body shape, the estimated body mass would be around 5–6 kg, with a shoulder height of only about 20 cm, comparable to a domestic standard sausage dog. The next earliest known proboscidean was *Phosphatherium escuilliei* (Gheerbrant et al. 1998, 2005). The nearly complete preserved cranium OCP DEK/GE 305 has a total length of around 170 mm (Gheerbrant et al. 2005), suggesting a shoulder height of around 30 cm and a body mass of about 17 kg. The larger and more derived *Daouitherium rebouli* (Gheerbrant et al. 2002) was more closely related to *Numidotherium* and *Barytherium* than to *Phosphatherium*, indicating an overall different body morphology, first; the true lophodont molar morphology of *Phosphatherium* is distinctive with respect to anthracobunids and sirenians (Gheerbrant et al. 1996, 1998); and second, the postcranial material of *Numidotherium* and *Barytherium* (Andrews 1906; Mahboubi et al. 1986) shows some typical characteristics of modern elephants, suggesting a shorter and more compact body from the level of *Daouitherium* onwards. The *Daouitherium* holotype (CPSGM MA4) mandible and teeth are about 10% smaller than the *Numidotherium koholense* mandible and teeth described by Mahboubi et al. (1986). The robust postcranial material of *Numidotherium* suggests that it was about 90–100 cm at the shoulders and probably weighed between 250 and 300 kg. *Daouitherium* was somewhat smaller, weighing probably around 200 kg. The postcranial material described by Andrews (1906) shows that *Barytherium grave* was about two times larger than *Numidotherium*, indicating a shoulder height in the flesh of 180–200 cm and probably over 2 tonnes. The abundant material of *Moeritherium* described by Andrews (1906) and Simons (1964) allows complete res-

Table 8. Relationship between shoulder height (in cm) and body mass (in tonnes) of fully grown adult proboscideans of different taxa in optimal conditions from below average to record-sized individuals.

		Grade 0: below average	Grade I: average min.–max. (mean)	Grade II: large	Grade III: very large	Grade IV: world record
Estimated percentage of the total population size		~ 5%	~ 90%	~ 5%	< 0.1%	< 0.001%
Loxodonta africana ♂	shoulder height	304 <	304–336 (320)	337–352	353–383	384–400
	body mass	5.2 <	5.2–6.9 (6)	6.9–7.7	7.7–9.5	9.5–10.6
Loxodonta africana ♀	shoulder height	247 <	247–273 (260)	274–286	287–311	312–325
	body mass	2.6 <	2.6–3.5 (3)	3.5–3.8	3.9–4.8	4.9–5.3
Loxodonta cyclotis ♂	shoulder height	209 <	209–231 (220)	232–242	243–263	264–275
	body mass	1.7 <	1.7–2.3 (2)	2.3–2.6	2.6–3.2	3.2–3.5
Mammuthus primigenius ♂ (North Siberian form)	shoulder height	266 <	266–294 (280)	295–308	309–335	336–350
	body mass	3.9 <	3.9–5.2 (4.5)	5.2–5.7	5.8–7.1	7.2–8.0
Mammuthus primigenius ♂ (European form)	shoulder height	299 <	299–331 (315)	332–346	347–377	378–394
	body mass	5.2 <	5.2–6.9 (6)	7.0–7.5	7.6–9.5	9.6–10.6
Mammuthus columbi ♂	shoulder height	356 <	356–394 (375)	395–413	414–449	450–469
	body mass	8.3 <	8.2–10.9 (9.5)	11–12.1	12.2–15.1	15.2–16.9
Mammuthus meridionalis ♂ *Mammuthus trogontherii* ♂	shoulder height	380 <	380–420 (400)	421–440	441–479	480–500
	body mass	9.6 <	9.6–12.7 (11)	12.8–14	14.1–17.4	17.5–19.5
Elephas maximus ♂	shoulder height	261 <	261–289 (275)	290–303	304–329	330–344
	body mass	3.5 <	3.5–4.6 (4)	4.6–5.1	5.2–6.3	6.4–7.1
Elephas maximus ♀	shoulder height	228 <	228–252 (240)	253–264	265–287	288–300
	body mass	2.3 <	2.3–3.1 (2.7)	3.1–3.4	3.5–4.2	4.3–4.8
Mammut borsoni ♂	shoulder height	389 <	389–431 (410)	432–451	452–492	493–513
	body mass	13.7 <	13.7–18.4 (16)	18.5–20.4	20.5–25.6	25.7–28.4
Mammut americanum ♂	shoulder height	275 <	275–305 (290)	306–319	320–348	349–363
	body mass	6.8 <	6.8–9.2 (8)	9.3–10.2	10.3–12.8	12.9–14.2
Deinotherium proavum ♂ and ♀	shoulder height	347 <	347–383 (365)	384–402	403–438	439–456
	body mass	9.1<	9.1–12.1 (10.5)	12.2–13.4	13.5–16.8	16.9–18.6
Palaeoloxodon antiquus ♂	shoulder height	380 <	380–420 (400)	421–440	441–479	480–500
	body mass	10.8 <	10.8–15 (13)	15.1–16.6	16.7–20.7	20.8–23

toration of the *M. lyonsi* species (Appendix 1: A). The nearly complete skull of a young individual, C.7867, was scaled up by 15% to fit with the postcranial material of different adult individuals described by Andrews (1906); the results show an extremely elongated animal 230 cm in length, only 70 cm at the shoulders in the flesh and with an estimated body mass of 235 kg (Appendix 1: A).

Deinotheres.—The members of the Deinotheriidae family were radically distinct from the above-described Plesielephantiformes. These animals were much larger, and their overall appearance was closer to modern elephants in terms of body shape and posture, except for the skull and mandible. The most plesiomorphic deinothere, *Chilgatherium harrisi*, was found in Ethiopia and was dated to the late Oligocene, ca. 28–27 Ma (Sanders et al. 2004). It was relatively small based on tooth size, probably less than 200 cm at the shoulders and about 1.5 tonnes of body mass. The later genus *Prodeinotherium* increased notably in size, the earliest species, *P. hobleyi*, was probably up to 270 cm and 4 tonnes judging by the size of the adult skull described by Harris (1973). The more derived European form *P. bavaricum* was of similar size; the fully grown male individual from Unterzolling (Huttunen and Göhlich 2002) has an estimated body mass of about 4.3 tons (Appendix 1: C). The nearly complete skeleton of *P. bavaricum* from Franzensbad (NHMW2000z0047/0001), is much smaller than the individual from Unterzolling by over a tonne (Appendix 1: B). The relatively small mandible and large pelvic apertura, where the ratio between the horizontal width of the pelvic apertura to the maximal pelvis breadth is 0.375, points in favour of the female gender, as similar ratios are found in female mammoth pelves (Lister 1996). However, such a comparison should be treated with caution due to the very separated taxa.

The largest forms of Deinotheriidae are within the last genus *Deinotherium*. The taxonomy of this genus has been somewhat chaotic for many decades (Gräf 1957; Bergounioux and Crouzel 1962; Harris 1973, 1978; Antoine 1994; Huttunen 2000; Markov 2008; Vergiev and Markov 2010; Böhme et al. 2012; Pickford and Pourabrishami 2013; Aiglstorfer et al. 2014). For this paper the morphospecies concept defended by Aiglstorfer et al. (2014) was followed, along with the African species (Arambourg 1934), which included the next species within the genus: *D. levius*, *D. giganteum*, *D. proavum* (= *D. gigantissimum* and *D. thraceiensis*) and *D. bozasi*. Moreover, the gigantic, nearly-complete specimen from Ezerovo, described by Kovachev and Nikolov (2006) as *D. thraceiensis,* is very problematic. This skeleton has many unique features among Proboscidea and is very different from other *Deinotherium* skeletons in several aspects. Firstly, the humerus/femur length ratio is 0.69, considerably less than the one observed in *D. proavum* specimens, where this ratio is always over 0.75, making the rear part much taller than the shoulders in the Ezerovo specimen (see Appendix 1: G, SOM: table 2). Secondly, the manus have much smaller metacarpals than other *Deinotherium* specimens despite its enormous overall body size. On the other hand, it has extremely elongated phalanges, a unique feature among Proboscidea. According to Dimitar Kovachev (personal communication 2011), he and his team found only 12 bones of the manus, including the fourth finger distal digit, which measured a striking 160 mm. Most noticeably, this skeleton has only 14 thoracic vertebrae and an outstanding number of 10 lumbar vertebrae. This composition has never been observed in any proboscidean, making it possible that the skeleton, in fact, represents at least two different individuals. However, this is not possible to confirm, in turn making a future rigorous study of the skeleton of high interest. Notwithstanding these observations, a restoration was made based on the description given by Kovachev and Nikolov (2006) (Fig. 7, Appendix 1) with some aspects being corrected. Namely, a comparative morphometric analysis with material described by Stefanescu (1910) seemed to indicate that the tibia and fibula had been restored too long, by 150 mm and 75 mm, respectively.

Several quite complete skeletons of *D. proavum* have been found (Stefanescu 1895, 1899, 1910; Tarabukin 1968; David and Shushpanov 1972; Bajgusheva and Tiskhov 1998; Bajgusheva and Titov 2006). All of them are practically identical in body size, around 365 cm at the shoulders and 10.5 tonnes of mass (Fig. 6, Appendix 1, SOM: table 1). Despite the gigantic size of these specimens, a partial skeleton excavated from 2002 to 2010 in Crete (Fassoulas and Iliopoulos 2011; Iliopoulos et al. 2014) may reveal an even larger individual, judging by the size of the metacarpal bones (AL unpublished data). The Greek specimen might attain a shoulder height in the flesh of 410 cm as well as an amazing body mass of over 14 tonnes, surpassing the size of the huge *D.* "*thraceiensis*" from Ezerovo.

The *D. giganteum* species was also of enormous size, fully grown individuals may reach 400 cm at the shoulders and 12 tonnes of body mass, making it two times heavier than the extant *Loxodonta africana* (Appendix 1: D, E). Christiansen (2004) calculated about one and a half tonnes more for this specimen. It must be noted that he erroneously calculated the average body mass as 14.6 tonnes whereas the correct average body mass according to his results is in fact 13.4 tonnes. The body mass obtained by allometric calculations is too excessive for the whole body volume of the animal; the relatively high body mass for its shoulder height and the probably more rapid locomotion of *Deinotherium* make its bones more sturdily built than expected. Finally, the African species, *D. bozasi*, also attained big size. The partial skull recovered from East Rudolf, Kenya (Harris 1976), probably belonged to an animal of over 360 cm at the shoulders in the flesh and 9 tonnes in body mass.

Mastodon ancestors.—The earliest Elephantiformes, including the genera *Hemimastodon*, *Palaeomastodon* and *Phiomia* (Shoshani and Tassy 2005), were middle-sized proboscideans similar in appearance to the first gomphotheres. A *Palaeomastodon beadnelli* femur described by Andrews (1906) measures 875 mm, suggesting a shoulder height in the flesh of about 220 cm and an estimated body mass of over 2.5 tonnes.

True mastodons.—The Mammutids, especially the species within the *Mammut* genus, were among the largest and most amazing proboscideans that ever lived. The Middle–Late Pliocene European species, *M. borsoni*, had the longest tusks among Proboscidea, measuring up to 502 cm outside the curvature (Mol and Logchem 2009). In terms of body size, they were also record-breakers, the composite restoration based on two not fully grown individuals of similar size (Milia I and Milia V), suggests an outstanding body mass of around 14 tonnes (Appendix 1: H). Several postcranial materials displayed at the municipal Natural History Museum of Milia indicate that fully grown specimens were considerably bigger. The glenoid cavity of a preserved distal part of a scapula is significantly larger than in Milia V (AL personal observation). Another complete massive left femur measures 1500 mm in length (Dick Mol personal communication 2012; AL personal observation); this specimen could have been up to 410 cm at the shoulders and 16 tonnes of body mass (Appendix 1: I), nearly three times the body mass of a fully grown African elephant. Despite these impressive figures, this was probably the average size for the species. On the other hand, the American species, *M. americanum*, was much smaller, although still very large compared to extant forms. It wasn't taller than living elephants, but it was much more robust. The rigorous restoration of the famous Warren mastodon (AMNH 9950) produces a body mass of nearly 8 tonnes at a shoulder height of only 289 cm (Appendix 1: J). The extreme breadth of the pelvis makes this animal extraordinarily massive. At the same shoulder height, *M. americanum* was up to 80% heavier than both extant elephant genera. Through the measurement of a particularly big femur, it was observed that large individuals weighed around 11 tonnes (Appendix 1: K).

Gomphotheres.—The diverse family Gomphotheriidae was composed of middle-sized to enormous animals, most of them very sturdily built. The well-known genus of *Gomphotherium* was composed of over ten species (Wang et al. 2013); most of them were comparable in size to the extant *Elephas maximus* (see Osborn 1936), but one European species, *G. steinheimense*, was much larger. The restoration of the complete skeleton found in Mühldorf (Göhlich 1998; Appendix 1: M) indicates that fully grown individuals grew to over 320 cm at the shoulders, and 7 tonnes in body mass. *G. osborni* was probably the most robust proboscidean that ever lived; its maximum pelvis breadth was twice its femur length (SOM: table 2), indicating an extremely wide body for the overall height of the animal. Moreover, its belly breadth was about three-quarters of its shoulder height.

The American shovel-tusker proboscideans (*Amebelodon*) were much larger than the Asiatic forms (*Platybelodon*) (see Osborn 1936). *Amebelodon britti* was about two times more massive than the extant Asian elephant, weighing around 8 tonnes (SOM: table 2). The North American *Stegomastodon mirificus* probably could have attained the shoulder height of the extant *E. maximus,* but with a greater body mass, of up to 6 tonnes. This inference is made given that, if we look at the restoration of a relatively young individual, we attain an animal of nearly 5 tonnes (Appendix 1: N).

The South American Gomphotheriidae have a very complex taxonomic history (Mothé et al. 2012; Lucas 2013). Nonetheless, a recent taxonomic revision based on well-preserved material allowed recognition of two species, *Notiomastodon platensis* and *Cuvieronius hyodon* (Mothé et al. 2014). The *Amahuacatherium peruvium* species recognized by Mothé et al. (2012) could be well placed into *N. platensis* or *C. hyodon* (Mothé et al. 2014). *Haplomastodon chimborazi* and *Stegomastodon platensis* are considered junior synonyms of *Notiomastodon platensis* (Mothé et al. 2012). *Notiomastodon* was probably much bigger than *Cuvieronius*, with large specimens reaching nearly 6.5 tonnes and 285 cm at the shoulders (SOM: table 2). The material described by Tapia-Ramírez et al. (2013), Osborn (1936), and Christiansen (2004) indicates that *Cuvieronius* was about 230 cm at the shoulders and 3.5 tonnes. The European *Tetralophodon*, *T. longirostris*, was of enormous size. However, the fairly complete adult skeleton found at Polinya was relatively small, as it was only 258 cm at the shoulders in the flesh (SOM: table 2), but the partial skeleton found at Villavieja del Cerro reveals a much larger animal, of about 345 cm at the shoulders in the flesh, and around 10 tonnes (SOM: table 2). Thus, the Polinya specimen might represent a female individual. Petrocchi (1954) described several cranial and postcranial materials from Sahabi in Lybia. Unfortunately, the bones are not catalogued to their corresponding species. A recent study (Boaz et al. 2008) determined that at Sahabi there are three proboscidean taxa: *Amebelodon*, *Anancus*, and *Stegotetrabelodon* (Elephantidae). The postcranial material described by Petrocchi (1954) indicates that proboscideans from Sahabi were very large, although their taxonomic identification is very difficult. The massive described humeri, measuring from 1000 to 1100 mm in length, were more attributable to *Amebelodon* or *Anancus*, given that the humerus of *Stegotetrabelodon* described by Maglio and Ricca (1977) was considerably more slender. These humeri suggest animals ranging from at least 310–350 cm at the shoulders and 7.5–10 tonnes or more in body mass. The listed ulnae lengths are not reliable based on other measurements of the same bones. The first five relatively short described femora are also very massive, being likely of *Amebelodon* or *Anancus*. On the other hand, a very long last femur, measuring 1470 mm in length, as well as two other very long tibiae, measuring 840 mm and 950 mm, respectively, may have belonged to *Stegotetrabelodon syrticus*. All these observations seem to indicate that *S. syrticus* might have surpassed 400 cm at the shoulders, and approached 11–12 tonnes in mass.

Stegodonts.—Stegodonts were small to gigantic proboscideans of Africa and Asia, living from the Pliocene to as late as the Holocene (Ma and Tang 1992; Saegusa 2001; van den Bergh 2008; Turvey et al. 2013). The smallest species was probably the island *Stegodon sondaari* (van den Bergh 1999; van den Bergh et al. 2008). A partial femur of an estimated length of 460 mm (van den Bergh 1999) indicates that this dwarf form was only 120 cm at the shoulders and 350–400 kg in body mass. *S. florensis* was considerably larger; a humerus (CV-72) measuring 630 mm in length (Hooijer 1972) indicates a shoulder height in the flesh of 200 cm and around 2 tonnes in body mass. *S. insignis* appears to be of similar size (Osborn 1942). The middle-sized *S. trigonocephalus* was up to 275–280 cm at the shoulders and over 5 tonnes according to a large humerus (RGM CD 4277) and femur (MBMa17337), measuring 850 and 1090 mm, respectively (Lomolino et al. 2013: appendix 1, table S7). Comparing the *S. zdanskyi* skull with the complete *S. ganesa* skull described by Falconer and Cautley in 1847 (see Osborn 1942), a shoulder height of about 310 cm is obtained, nearly the same as proposed by Osborn (1942), suggesting a body mass of about 6.5 tonnes. The largest species was probably the huge *S. zdanskyi*, with fully grown adults weighing as much as 13 tonnes (Appendix 1: Q).

Palaeoloxodonts.—The generic name of *Palaeoloxodon* was first introduced by Matsumoto (1924). However, there has been controversy on whether species of this genus should be classified as *Elephas*, *Elephas* (*Palaeoloxodon*), or *Palaeoloxodon* (Maglio 1973; Beden 1979; Shoshani and Tassy 1996). Recently, different studies focusing on cranial observations concluded that *Palaeoloxodon* is a bona fide genus (Inuzuka and Takashi 2004; Shoshani and Tassy 2005; Shoshani et al. 2007).

These animals were among the smallest and the largest Proboscidea. The *P. falconeri* was the smallest *Palaeoloxodon*; the material from Spinagallo Cave described by Ambrosetti (1968) indicates that these island proboscideans were only up to 100 cm at the shoulders and close to 300 kg in body mass, about 115% heavier than the expected body mass for the same shoulder height in extant *L. africana* male calves (Dale 2010). This is due to the most robust morph of dwarf adults. Another dwarf elephant from Tilos, *P. tiliensis*, was substantially larger, the excavated femora of up to 700 mm (Theodorou et al. 2007) indicate that the Tilos elephant was around 185 cm at the shoulders and 1.3 tonnes in body mass. The medium-sized species, *P. mnaidriensis*, was over 200 cm at the shoulders and around 1.7 tonnes in body mass according to the material recovered from Puntali Cave (Ferretti 2007), although very large-sized specimens may be within the species, such as those found at the Contrada

Fusco in association with middle-sized *P. mnaidriensis* remains. Among them is a very large humerus of 1032 mm in length (Chilardi 2001), indicating a shoulder height of up to 320 cm, and a body mass of 6.5 tonnes. Such enormous differences may discard the possibility of these dimensions being due to sexual dimorphism. Larger specimens were in fact probably *P. antiquus*. In any case, further research of the material will be needed in order to resolve this question.

The first palaeoloxodonts were huge. The remains of the African long-limbed *P. recki* found in the Koobi Fora Formation produced an animal of 427 cm at the shoulders and 12.3 tonnes in body mass (Appendix 1: T). This specimen was still a growing animal judging by the stage of the molars and by the fusion of the femur proximal epiphyses. Fully grown male individuals from this area may have surpassed 450 cm at the shoulders and reached 14–15 tonnes in body mass. The later and enormous European form *P. antiquus* was more massively built average fully grown male individuals in optimal conditions were around 400 cm at the shoulders and 13 tonnes in mass (Table 8). Considerably larger individuals appear to have been found, although the restored Taubach's skeleton femur at 1600 mm, mentioned by Osborn (1942) and Christiansen (2004), is clearly exaggerated because its humerus and tibia are around 1300 mm and 900 mm in length, respectively (Dietrich 1916), indicating that the correct length should be around 1500 mm or less (SOM: table 2). On the other hand, the large Upnor specimen was 404 cm at the shoulders when he died (SOM: table 2); he was quite a young adult individual of about 35 years as only the ridge-plates of the second molars are in use (Osborn 1942). He may have continued growing for another 15 years. According to the growth of extant proboscideans, elephants appear to grow about 15–20 mm on average per year during the last 15–20 years of growth (see Laws et al. 1975; Sukumar et al. 1988; Lee and Moss 1995; Kurt and Kumarasinghe 1998; Shrader et al. 2006). Thus, the Upnor specimen may have attained over 435 cm at the shoulders and 16 tonnes in body mass if he had lived longer. The enormous Montreuil humerus (Adams 1877) indicates a large bull approaching 15 tonnes in body mass (Appendix 1: W). Moreover, in 1847 and 1850, two or more *P. antiquus* skeletons were unearthed from San Isidro del Campo (Graells 1897). Among the recovered remains was a colossal, perfectly preserved pelvis. From its size, it can hardly be attributed to most of the other material, the maximum horizontal pelvic girdle width was measured at the astounding size of 2350 mm (Graells 1897). Osborn (1942) considered this measurement erroneous, but other measurements of the pelvis (horizontal width of pelvic aperture: 700 mm) and the good drawings that figure in Graells' plates (1897) suggest that the measurement is reliable. An explanation for the extreme breadth of the pelvis is probably that the measurement was taken with both wings lying on the floor, in an angle too wide, misrepresenting the real breadth (both halves are not fused; see Graells 1897: pl. 18). Thus, the maximum width in the anatomical position could have been "only" around 2100−2150 mm. This measurement is in relative accordance with the other pelvic measurements with the Viterbo specimens (see Palombo and Villa 2003; Appendix 1: V). The Iberian specimen was all in all about 20% larger than the Italian ones. A gigantic tibia measuring 1070 mm in length was also described by Graells (1897) and fits perfectly with the enormous pelvis's corrected breadth, so a *P. antiquus* of these proportions would have been 460 cm at the shoulders and over 19 tonnes in body mass. Unfortunately most of the remains of these skeletons were destroyed during repeated transfers (Graells 1897). Thus it is not possible to verify the huge size of the animal, so the size estimation of the animal should be treated with caution.

Femur proportions suggest that the Asian species, P. *namadicus*, may have been even larger than its European cousin, though perhaps not as bulky (Table 9). A recently described femur (GSI/CR/PAL/A/566), found in the Narmada River basin in India, is 1490 mm long (Meshram and Sonakia 2006), indicating that a living specimen would have stood close to 400 cm at the shoulder. Even larger remains were discovered throughout the 19th and early 20th centuries (Prinsep 1834; Spilsbury 1837; Falconer and Cautley 1846; Falconer and Walker 1859; Pilgrim 1905). Pilgrim (1905) described the partial skeleton of a *P. namadicus* that was found amongst alluvial deposits of the Godavari River at Nandur. The skull and the postcranial material indicates that the remains had belonged to a very large elephant. Both femora were found, but fragmented. Pilgrim (1905) estimated the total length of the femur to be about 69 inches, or 1750 mm. This estimate was too high: the preserved remains suggest that the total length of the femur is closer

Table 9. Measurements (in mm) of femora of different *Palaeoloxodon* specimens; e, estimated.

	Palaeoloxodon antiquus		*Palaeoloxodon namadicus*		
	Konin Jakubowski (1988)	AMPG 1960/32 Melentis (1963)	GSI/CR/PAL/A/566 Meshram and Sonakia (2006)	Sagauni I Prinsep (1834)	Nandur Pilgrim (1905)
Proximal width	470	476	434	457	483
Minimun shaft width	157	170	183	190e	–
Minimum shaft thickness	130	117	115	–	–
Least circumference of the shaft	–	478	–	483	520
Breadth of the condyles	275	–	260	279	–
Distal breadth	323	298	291	–	305
Greatest length	1429	1372	1490	1600	1650e

to 1650 mm—a considerable length nonetheless. The living animal would have been around 450 cm at the shoulders.

Another gigantic skull found decades earlier may have belonged to an even larger individual; however, this skull was never described scientifically and its whereabouts are now unknown (Pilgrim 1905; Khatri 1966). General Twemlow, who discovered the skull, wrote only a short manuscript about it, though it may have also been studied by Falconer (Pilgrim 1905). This specimen's tusks had a circumference of 737 mm, 17% larger than the tusks of the specimen described by Pilgrim (1905).

The other remains found throughout the nineteenth century suggest that *P. namadicus* was indeed titanitc (Prinsep 1834; Spilsbury 1837; Falconer and Cautley 1846; Falconer and Walker 1859). Several enormous remains reported by Prinsep (1834) and Spilbury (1837) were later assigned to *Elephas namadicus* (a synonym of *Palaeoloxodon namadicus*) by Falconer and Cautley (1846; Falconer and Walker 1859). Prinsep (1834) described two giant femora from Sagauni at Narsinghpur district, India. Before being removed from the earth, the left femur full length was found to be 1600 mm (Prinsep 1834; Falconer and Walker 1859). Not long after, Spilsbury (1837) described a left ulna and a right humerus that had likely belonged to the same elephant. Both samples were collected from the same location; the fossil sizes also correspond to the same individual (Spilsbury 1837; Falconer and Walker 1859). According to measurements by Spilsbury (1837) and Falconer and Walker (1859), the humerus length from the caput to the articular surface was 1400 mm with a maximum length of nearly 1450 mm, while the maximum length of the ulna was 1270–1295 mm. The size of these remains indicates that this individual must had measured 435 cm or more at the shoulders in life.

The dimensions and slender proportions of these limbs are similar to those of the gigantic *P. recki* skeleton from Koobi Fora, suggesting a proportionally similar body bulk. The Sagauni elephant, therefore, was likely to have had a body mass of about 13 tonnes. Surprisingly, the right proximal femoral head of the Sagauni elephant's femur is entirely detached, indicating a young animal would have continued to grow considerably more if it had lived longer. But that's not all: a femur distal part of a second elephant reported by Prinsep (1834), is nearly one-quarter larger than the preceding individual's femur (Prinsep 1834). Assuming that the portion was only 20% larger, the complete femur could have been up to 1900 mm in length. This immense elephant would have stood 520 cm at the shoulders with a probable body mass of over 22 tonnes (Appendix 1: AH), surpassing dinosaur sauropods such as *Camarasaurus lentus* and *Apatosaurus louisae*, and doubling *Diplodocus carnegii* in mass (Paul 1997). The distal femur portion of this specimen must be restudied. The fossils are likely stored in the Indian Museum of Kolkata; until such a collection can be revised, this size estimate will remain speculative.

Another remarkably large proximal portion of a humerus, also assigned to *P. namadicus*, was found within Narmada alluvial deposits (Falconer and Cautley 1846). Its proximal epiphysis is not entirely fused (Falconer and Cautley 1846: pl. 48: 1). The preserved fragment is 750 mm long (Falconer and Cautley 1846), which is only about half the length of the humerus.

Mammoths.—The successful group of mammoths included at least ten species, most of them of a very big size. The first representative was *Mammuthus subplanifrons*. The remains that Maglio (1970) used to create the *Loxodonta adaurora* species probably belong to *Mammuthus subplanifrons*. Todd (2010) considered *L. adaurora* as a junior synonym of *M. subplanifrons*. The postcranial material described by Maglio (1970) and by Maglio and Ricca (1977) also corroborates Todd's (2010) conclusions. The posterior thoracic and lumbar vertebrae processus spinosus proportions of the KNM KP-385 holotype specimen are clearly *Mammuthus* type; the lengths of spines decrease dramatically unlike in *Loxodonta*, whose lengths in this section increase considerably. The KNM KP-397 specimen, of a similar size to the holotype, has a relatively low ratio between the tibia and femur lengths (0.565), which is very common in *Mammuthus*. Finally, the composite restoration of both similar-sized specimens produces the typical mammoth body shape (Appendix 1: X). The size of the earliest representative mammoth was very big, over two times heavier than the extant *Elephas maximus*.

Mammoths appear to have continued to increase in size. The first Western European remains dated from the late Middle Pliocene; 2.6 Ma (Palombo and Ferretti 2004) are very large. A partial skeleton from Laiatico described by Ramaccioni (1936), which is referred to as "*M. rumanus/meridionalis*" (Palombo and Ferretti 2004), was huge, the right tusk has a diameter of 260 mm near to the proximal part, with a total length of 335 cm. The humerus was found to be in poor condition but was restored completely to 1450 mm in length (Ramaccioni 1936; Palombo and Ferreti 2004), although judging by the size of the rest of the postcranial material found (Ramaccioni 1936), the humerus was probably erroneously restored and the size of the animal should be about 10% lesser. In any case, the animal would have been very large at 10–11 tonnes in body mass.

The Early–Middle Pleistocene *M. meridionalis* and *M. trogontherii* were also huge, a shoulder height of 400 cm and a body mass of 11 tonnes were common for these species (Table 8, SOM: table 2). A distal part of a humerus found at Monte Sacro (Maccagno 1962) was over 7% larger than the magnificent Scoppito *M. meridionalis* humerus (Appendix 1: Y). Assuming *M. meridionalis* identity and not *Palaeoloxodon antiquus*, a shoulder height close to 430 cm and 13 tonnes of body mass are obtained. Several other large remains from Mundesley, including a huge femur, are attributed to *M. meridionalis* (Falconer 1868; Adams 1881; McWilliams 1967; Mol et al. 1999). These remains include an enormous humerus (No. 200) with an articular length of 1300–1346 mm (Falconer 1868; Adams 1881; Gunn 1891), a

Fig. 11. Left humerus of giant Mosbach mammoth (MNHM PW1947/23) from Middle Pleistocene, Mosbach, Germany; in lateral view.

very large radius, 990 mm in length, found very near the humerus (Adams 1881; Gunn 1891), a giant femur of 1524 mm in length that was found in conjunction with the humerus and radius (Adams 1881; Gunn 1891; McWilliams 1967) and a large pelvis half (No. 225) found at the same place, which, if it was complete, would have a maximum pelvis breadth of nearly 1800 mm. These specimens correspond very much in general proportions, so it is very possible that they belonged to the same individual. The great Mundesley mammoth would therefore have been about 415 cm at the shoulders and 12 tonnes in body mass. Another specimen was found in the same place as of the above material, a left lower jaw (Gunn Collection No. 361) of an adult but still growing 40-year-old animal that included the third molar, which, according to Gunn (1891), was different from *M. meridionalis*, *M. primigenius*, and *P. antiquus*, while the ramus was something intermediate between *M. meridionalis* and *M. primigenius*. The complete plate number of the M3 was 18, which falls within the range for *M. trogontherii* (Wei 2010) and excludes *M. meridionalis* and *M. primigenius* identity. This partial jaw could be perfectly associated with the above material (Gunn 1891), so that the Mundesley mammoth was likely from *M. trogontherii* species. Falconer, Adams, and Gunn's (1868, 1881, 1891) misidentification of this specimen might have been because *M. trogontherii* was unknown to them at that time as the species wasn't described until 1885 by Pohlig.

Another gigantic third metacarpal mentioned by Adams (1881: 221) was 270 mm in length, and it probably belonged to a *M. meridionalis* or *M. trogontherii* of 420 cm at the shoulders and 12.5 tonnes in body mass.

In 1922, an enormous left humerus was recovered from the Mosbach site and stored at the Natural History Museum of Mainz, Germany (Schmidtgen 1926). Today this humerus is labelled MNHM PW1947/23. The preservation of the bone is fairly good (personal observation), and only a few parts are reconstructed in plaster, including some parts of the shaft and the proximal portion (Fig. 11). Apparently the humerus was probably found or extracted in different parts but it was accurately restored (especially the diaphysis). The proximal and distal epyphises are well fused, indicating an old animal of probably more than 50 years.

This humerus is probably the longest ever found among Proboscidea (Table 10). The maximal length is 1463 mm, and it could have been even longer as the greater tubercle was probably restored too short, by ~20 mm. This humerus was first identified as *Mammuthus trogontherii* (Schmidtgen 1926; Mol and Lacombat 2009) although Lister (2010) later questioned it. The humerus was discovered in Middle Pleistocene river sediments, making the identity of the specimen as *Mammuthus* or *Palaeoloxodon* not clear. But the slenderness of the piece and the poorly developed rugose muscle scars of this humerus favour the *Mammuthus* identity (European palaeoloxodonts' humeri are much more powerfully built than mammoth ones).

Taking into account the extreme length of the humerus, it can be plausibly identified as one of the following two mammoth species: *M. meridionalis* and *M. trogontherii*. However, *M. meridionalis* can be discarded as it disappeared during the Early Pleistocene. This giant humerus seems to thus come from a very large *M. trogontherii*. Based on the obtained ratios between humerus lengths and shoulder heights for this species, the shoulder height of this animal in the flesh must have been very close to 450 cm (Fig. 3 and Table 3).

Table 10. Measurements (in mm) of the left humerus of the giant *Mammuthus trogontherii* (MNHM PW1947/23) from Mosbach.

Greatest length	1463
Length to caput	1440
Physiological length	1417
Proximal width	392
Maximum proximal thickness	435
Minimum width of the saft	173e
Least circumference	550
Distal width	370
Distal thickness	245
Width trochlea	306

Table 11. Measurements (in mm) of maximal lengths of pelvic bones and humeri of different *Mammuthus* specimens; >, over.

Species	Individual	Humerus	Pelvis	Reference
Mammuthus columbi	AMNH 9950	>1120	1120	Osborn 1942
	DMNH 1359	1240	1350	Osborn 1942
Mammuthus meridionalis	Rodionovo	1260	1370	Maschenko et al. 2011
	Scoppito	1320	1330	Maccagno 1962
Mammuthus trogontherii	Zhalainuoer III	1274	1286	Larramendi 2014
	Mosbach	1463	>1470	Schmidtgen 1926

Another very interesting piece was recovered from the same sandpit a year after the discovery of the humerus, a complete and very large male pelvis (Schmidtgen 1926). The maximal breadth of the pelvis was 1830 mm, indicating a big-sized mammoth of about 415 cm at shoulder height in the flesh. Otherwise, the other recorded measurements probably reveal a considerably taller mammoth, the maximal length of the pelvis is 1470 mm, while the pubis is not entirely preserved. This measurement is very close to the maximal humerus length of the giant humerus. In mammoths, the greatest length of the humerus usually corresponds with the greatest length of the pelvis (Table 11). The pelvis was found in the same layer as the humerus, a mere 15 metres away from it (Schmidtgen 1926). It is likely that both elements represent the same animal; if so, this discovery provides important information, the slenderness of the humerus and the relatively narrow pelvis support the idea of a strong negative body size allometry in exceptionally tall animals. The calculated body mass for this individual is 14.3 tonnes (see Appendix 1: AA), indicating a strong negative allometric growth. The result is only 4% less than predicted by the shoulder height-body mass formula proposed in this study (Table 7).

More remains recovered from Mosbach are stored in the Wiesbaden Museum collection. A huge *M. trogontherii* right femur (MWNH GP MOS 507) lacking the proximal part measures 1325 mm; the estimated total length would be over 1500 mm, indicating that the animal was about 410 cm at the shoulders and nearly 12 tonnes in mass. Several stored partial tusks over 250 mm in diameter indicate individuals approaching 400 cm at the shoulders.

Other gigantic material recovered in the 1980s in Zhalainouer, northern China, show again the huge size of *M. trogontherii* (Larramendi 2014). A massively built humerus stored in the Inner Mongolian Museum collection is broken into two pieces. The greatest distal width of the distal part is 400 mm (AL personal observation), 30 mm more than the Mosbach humerus. The maximal length of the Chinese specimen is probably shorter, at around 1400 mm. The giant Zhalainouer specimen (430 cm at the shoulders) was not as tall as the one at Mosbach but probably reached over 13.5 tonnes in mass, approaching the more slender European mammoth.

The Columbian mammoth *M. columbi* (= *M. imperator*; Agenbroad 2005), although large, was smaller than its ancestral *M. trogontherii* (Harington 1984; Wei 2010). The average size for the species was about 375 cm at the shoulders and 9.5 tonnes in body mass (Table 8), although a particularly big tibia indicates a specimen approaching 12.5 tonnes in mass (Appendix 1: AB, AC). Other specimens attributed to *Mammuthus jeffersonii*, may have represented hybrids between *M. columbi* and *M. primigenius* (Enk et al. 2011) and attained an intermediate size between two species (SOM: table 2).

The Channel Island small mammoth, *M. exilis*, evolved from *M. columbi* (Agenbroad 2012) and was nearly five times smaller. The largest individual represented by a large pelvis of 942 mm in breadth (Agenbroad 2002) probably belonged to a big individual of 230 cm at the shoulders and 2 tonnes in body mass. A large humerus measuring 833 mm in length used by Roth (1990) is more likely to represent a small female of *M. columbi* (Agenbroad 2009).

The renowned Woolly mammoth, *M. primigenius*, was probably the most successful mammoth that occupied the whole of Eurasia and North America. The European form was considerably larger than North Siberian specimens, surpassing 6 tonnes in body mass and 315 cm at the shoulders on average, with particulary big specimens exceeding 8 tonnes in mass (Apendix 1: AE, SOM: table 2). The northern Woolly mammoths were about the same height as modern Asian elephants, although proportionally a bit heavier (Table 8). The last *M. primigenius* that survived in Wrangel Island was of similar size; a pelvis measuring 1300 mm in breadth (Tikhonov et al. 2003) indicates that bulls approached 280 cm at the shoulders and 4.5 tonnes in body mass. Three tibiae from the Wiesbaden Museum collection (AL personal observation) and 13 from the Naturalis Biodiversity Center (Lomolino et al. 2013) are labelled as *M. primigenius.* Their lengths easily surpassed 700 mm, indicating individuals exceeding 330 cm and approaching 350 cm at the shoulders; so the species identification for these bones should be treated with caution, as many of them might well have belonged to other species such as *M. trogontherii* (probably female individuals). A particularly large tibia (RGM ST445385) labelled as *M. primigenius* measured 870 mm in length (Lomolino et al. 2013). This is hardly possible and may have belonged to a fully-grown *M. trogontherii* bull close to 400 cm at the shoulders. A humerus identified as *M. primigenius* has the greatest length of 1225 mm (Christiansen 2004), indicating a shoulder height of over 375 cm. Again it is very possible that the humerus was erroneously catalogued. Another enormous partial skull from Flaminia was described as *M. primigenius* (Palombo 1972), but according to enamel thickness, lamellar frequency, and size, it is more likely to have been *M. trogontherii*. On the other hand, the giant *M. primigenius fraasi* from Steinheim (Dietrich 1912) was very large, it attained a shoulder height in the flesh of 389 cm, and a body mass of about 9.5 tonnes (SOM: table 2). The relatively low body weight for its shoulder height is due to its pelvis being extremely narrow, only 1400 mm in breadth (Schmidtgen 1926), although it may lack the iliac crest epiphysis (see Dietrich 1912: fig. 20), and the total breadth would in fact have been around 1500 mm including the epiphysis. At any rate, the ribs of this specimen were very long, so the belly was probably considerably wider than the pelvic region, unlike the rest of the mammoths. The Steinheim mammoth seems to be an intermediate between *M. trogontherii* and *M. primigenius*, and, according to some authors (Lister and Stuart 2010), this specimen should be referred to as *M. trogontherii*. According to others, it should just be placed as *M. primigenius* (Dick Mol, personal communication 2011).

Not all mammoths were middle- to giant-sized creatures, dwarf forms also occurred. The *M. lamarmorai* from Sardinia island was only 140 cm at the shoulders and 550 kg in body mass, based on a humerus described by Palombo et al. (2012) that has an articular length of 450 mm. Smaller still was *M. creticus*; the maximum humerus length of an adult specimen was 330 mm (Herridge and Lister 2012), indicating a shoulder height of 100 cm and a body mass of about 180 kg, making the Cretan mammoth the smallest elephantid ever found.

Largest land mammal

It is believed that the largest land mammal that ever lived was the huge indricothere hornless rhinoceros. Today at least two genera are recognized within the large indricotheres: *Paraceratherium*, and *Dzungariotherium* (Prothero 2012: 85). *Paraceratherium transouralicum* appears to be the biggest species (Granger and Gregory 1936; Fortelius and Kappelman 1993; Paul 1997). The largest remains are represented by three specimens: two giant cervical vertebrae (AMNH 2618) and a partial central metacarpal (AMNH 26175) (Fortelius and Kappelman 1993; Paul 1997). An accurate volumetric restoration based on more complete specimens and extrapolated to the largest remains, produces a giant *Paraceratherium* of 480 cm at the shoulders and 16.4 tonnes in body mass (Paul 1997). The SG used by Paul (1997) was 0.95, indicating a total volume of 17.3 m^3. Applying a more reliable SG of 0.99, a body mass of 17.1 tonnes is obtained. The GDI method was also applied in Paul's (1997) reconstruction, producing a very similar body mass of 17.4 tonnes. A body mass of around 17 tonnes is therefore expected for the largest *Paraceratherium* bulls. Other huge parts of the left ramus including p4–m2 and M3 found in Sinkiang (Chow and Xu 1959) are of enormous dimensions. Chiu (1962) created the new species *Paraceratherium tienshanense* on the basis of these remains, and according to Qiu and Wang's (2007) recent comparative study, the species should be placed into the genus of *Dzungariotherium*. A complete *Dzungariotherium orgosense* skull and other material described by Chiu (1973) enable comparison. The skull is 121 cm in condylo-basal length, and this would indicate a shoulder height of about 420 cm if this species had similar body proportions to *Paraceratherium transouralicum*. The M3 and the m2 of *D. tienshanense*, are 23% and 17% longer than *D. orgosense*, respectively, although much narrower (see Qiu et al. 2004; Qiu and Wang 2007). A priori the material of *D. tienshanense* may indicates a huge animal, but the third metatarsal associated with the skull of *D. orgosense* is only 400 mm in length (Chiu 1973). Thus, the *D. tienshanense* metatarsal could have been about 480 mm in length, 25% less than estimated for the largest *Paraceratherium* (Granger and Gregory 1936; Gingerich 1990). Therefore, *Dzungariotherium* had proportionally larger teeth and skull than *Paraceratherium* but a smaller body. Some proboscideans appear to have approached the dimensions of the largest indricotheres: the average body size of *Mammut borsoni* was very close to the largest *Paraceratherium*, and big bulls may have exceeded the latter's body mass. The Milia 5 individual (Appendix 1: I) was only about 30 years old and weighed around 14 tonnes; had he lived longer until 50 years of age, and had he grown at the same rate as modern elephants, he might have approached and even surpassed 18 tonnes in body mass. The impressive *P. namadicus* remains (Prinsep 1834), suggest that fully grown bulls may have been about 5 tonnes heavier and 40 cm taller at the shoulders than the biggest indricotheres. Thus, the title of the largest land mammal that ever existed seems to be now within the order of Proboscidea. Moreover, based on solid evidence gathered from indricothere remains (limb bones such as humerus, ulna, radius, femur, or tibia, and partial skeletons) (see Borissiak 1917; Granger and Gregory 1936; Gromova 1959; Wang 2007; Antoine et al. 2008), the size of *Paraceratherium* was surpassed by many proboscidean especies known from partial to nearly complete skeletons. The composite skeleton restored by Paul (1997) weighed 8 tonnes, and most large indricothere skeletons and bones indicate that they share a similar body mass, with the largest individuals probably approaching only about 10 tonnes.

Conclusions

The results of this study reveal that the volumetric method, provided that the models are technically correct, is superior to the allometric one. This is not merely because of the more reliable results of the former method, but also due to the fact that the volumetric method can provide other important information about the studied specimens, such as animals' life appearance, posture, and body dimensions (e.g., heights, lengths, breadths). The present results could contribute to future research works on the energetics, physiology, ecology, population density, functional anatomy and phylogeny of extinct proboscideans. The equations developed here will also be very useful for calculating the size (shoulder height and body mass) of past and new proboscidean findings in a quick and simple manner.

Most of the published extinct proboscidean shoulder heights in the bibliography, which are generally based on incorrectly mounted skeletons or on erroneus percentages of the bones related to the shoulder heights, are concluded to be inaccurate.

Several species were considerably larger than previously thought. The upper size for land mammals of 20 tonnes, proposed by Economos (1981) based on the gravitational tolerance of extant animals, was probably surpassed by the largest proboscidean species within the genera *Palaeoloxodon* and *Mammut* genera. *Paraceratherium* appears not to be the largest land mammal ever. Mammoths were relatively as heavy as, or even heavier than, extant *Elephas*, contrary to the conclusion drawn by Christiansen (2004). The prevalent idea that *Elephas maximus* is much heavier than *Loxodonta africana* at any given shoulder height is rejected.

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Appendix 1

Proboscidean skeletal restorations and body mass estimates

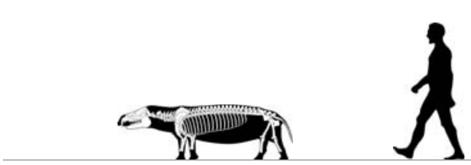
All skeletal restorations are presented on the same scale (1/100). The human figure is 180 cm tall. Mass estimates are in kilograms (kg) for small proboscideans and in tonnes (t) for the larger forms. The age is in years, pelvis breadth, femur and humerus greatest lengths are in mm (* refers to the humerus articular length). The listed shoulder heights correspond to the standing position of each animal. The body masses calculated for *Mammuthus primigenius* and *M. trogontherii* have the total hair weight included. The pelvis breadth of *Deinotherium proavum* from Manzati was corrected from Stefanescu (1910); he estimated it at 2080 mm, but the other measurements of the pelvis and good illustrations of the plates indicate about 150 mm less. The Brussels mammoth skull (see Dietrich 1912) and the beautifully preserved skull of *M. meridionalis* from Liventsovka (Garutt et al. 1977), were scaled up by 5% to fit the *Mammuthus primigenius* (Siegsdorf) and *Mammuthus meridionalis* (Scoppito) skeletons, respectively. The *Paraceratherium* silhouette was modified from Paul (1997). Abbreviations: BM, body mass; SH, shoulder heights; t, tonnes; e, estimated (margin error: ±2%); ~, around (margin error: ±5% in shoulder height and ±20% in body mass). The partial bones restored to its full size are shaded in grey. Note: The skeleton of *Deinotherium* "*thraceiensis*" may be composed of two or more individuals. The estimated body size for *Paraceratherium transouralicum* (AMNH 26168/75) and *Palaeoloxodon namadicus* (Sagauni II), should be taken with a grain of salt.

Moeritherium

M. lyonsi Qasr-el-Sagha

sex – age adult size group –
humerus 240 femur 270 pelvis –

A



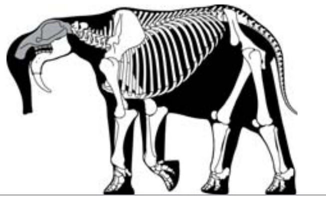
SH 70 cm • BM 235 kg

Prodeinotherium

P. bavaricum NHMW2000-z0047/0001

sex female? age adult size group –
humerus 790* femur 1055 pelvis 1200

B

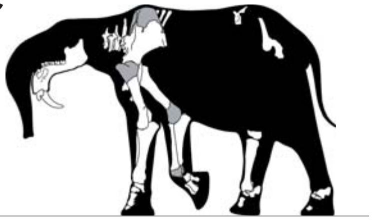


SH 247 cm • BM 3.1 t

P. bavaricum Unterzolling

sex male age adult size group –
humerus 890e femur – pelvis –

C



SH 278 cm • BM ~4.3 t

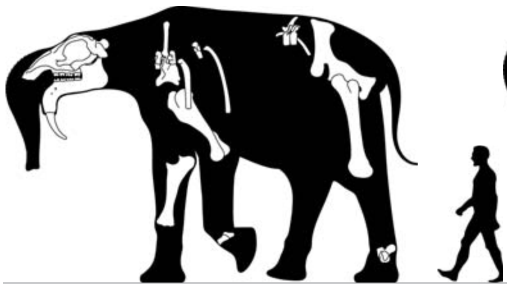
2 m

Deinotherium

D. giganteum 1935I 23 and Eppelsheim skull

sex – age adult size group –
humerus 1090* femur 1380 pelvis 1750e

D

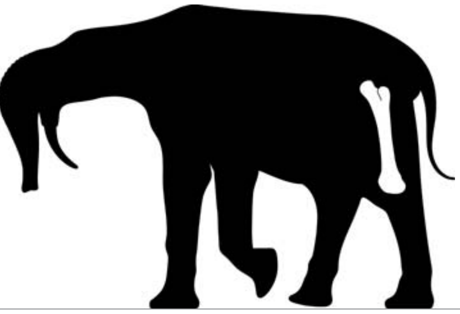


SH 363 cm • BM ~8.8 t

D. giganteum Eppelsheim (after Christiansen 2004)

sex male? age adult size group –
humerus – femur 1515 pelvis –

E

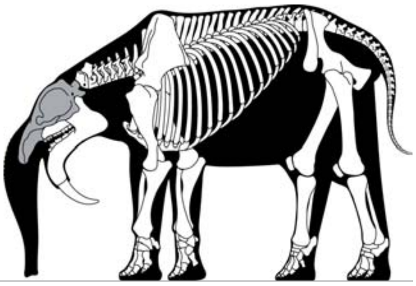


SH ~400 cm • BM ~12 t

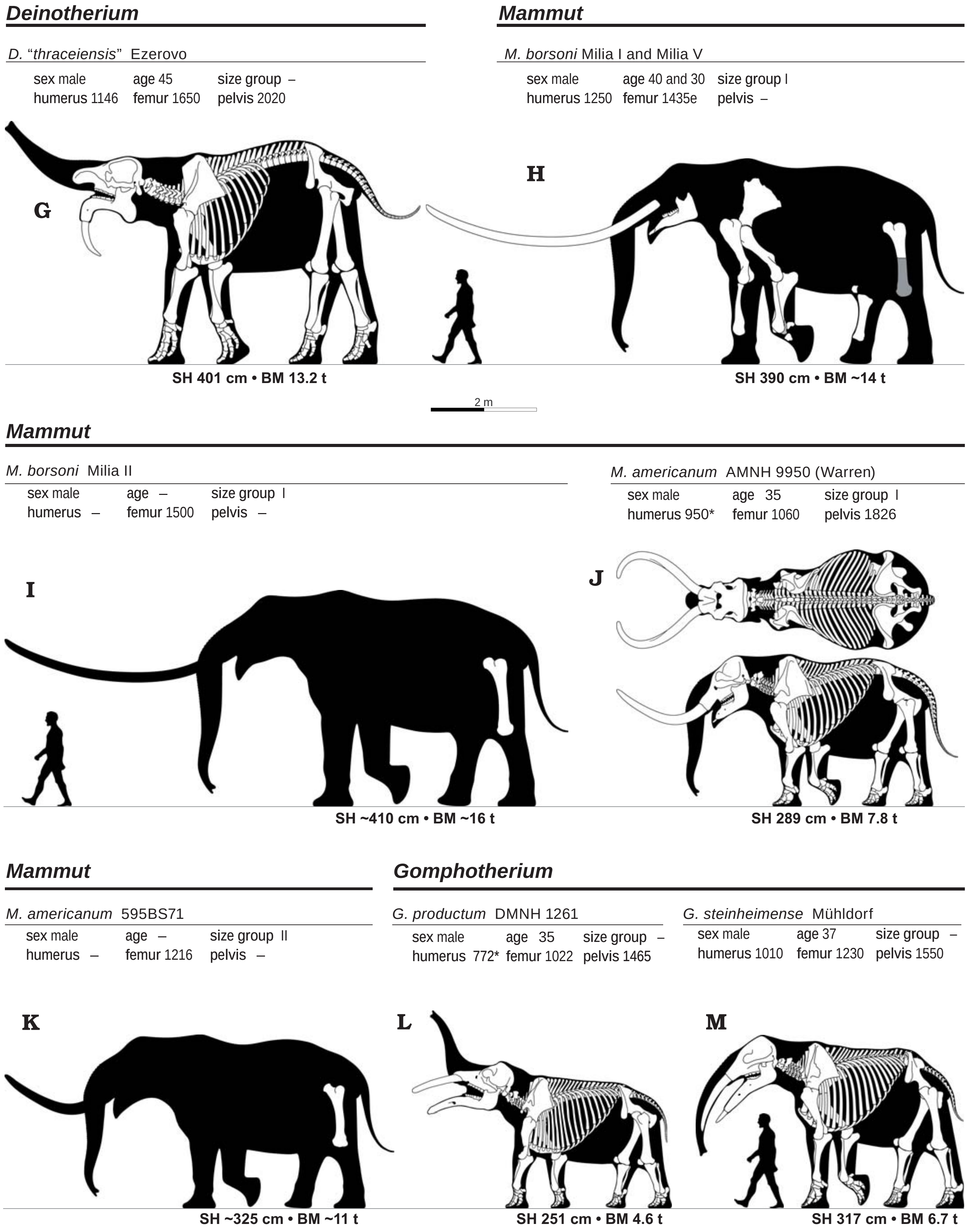
D. proavum Manzati

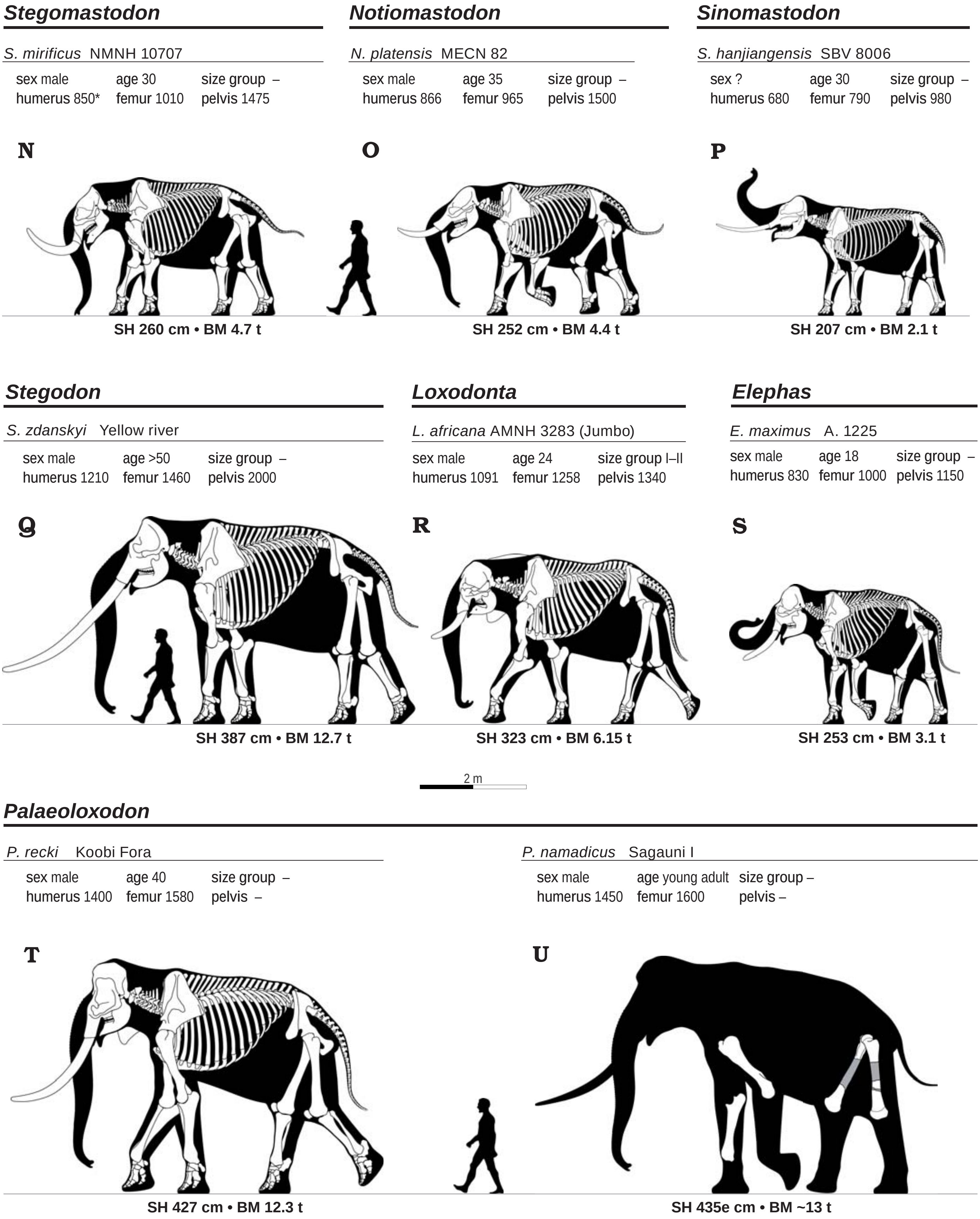
sex male age adult size group I
humerus 1100* femur 1440 pelvis 1930

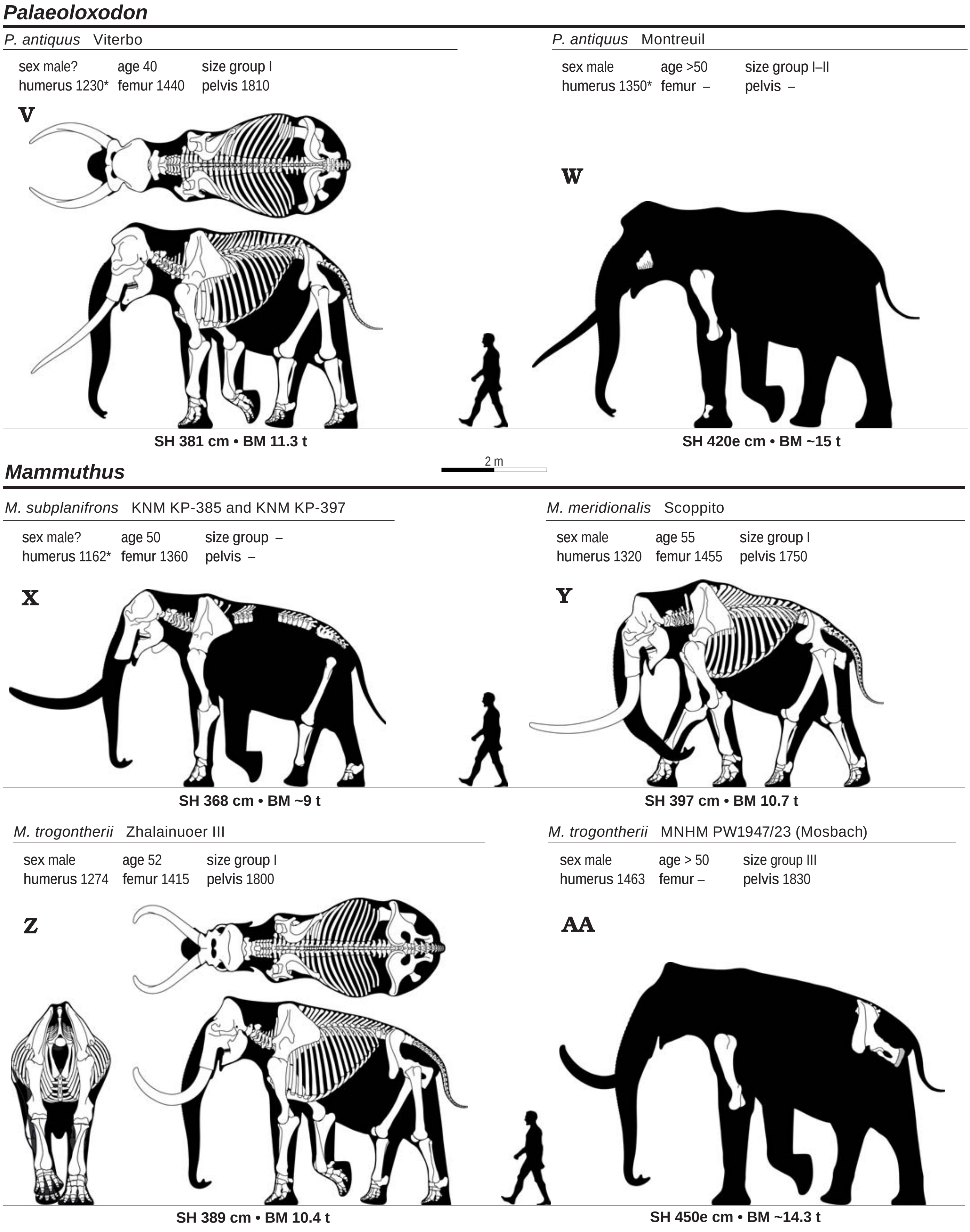
F

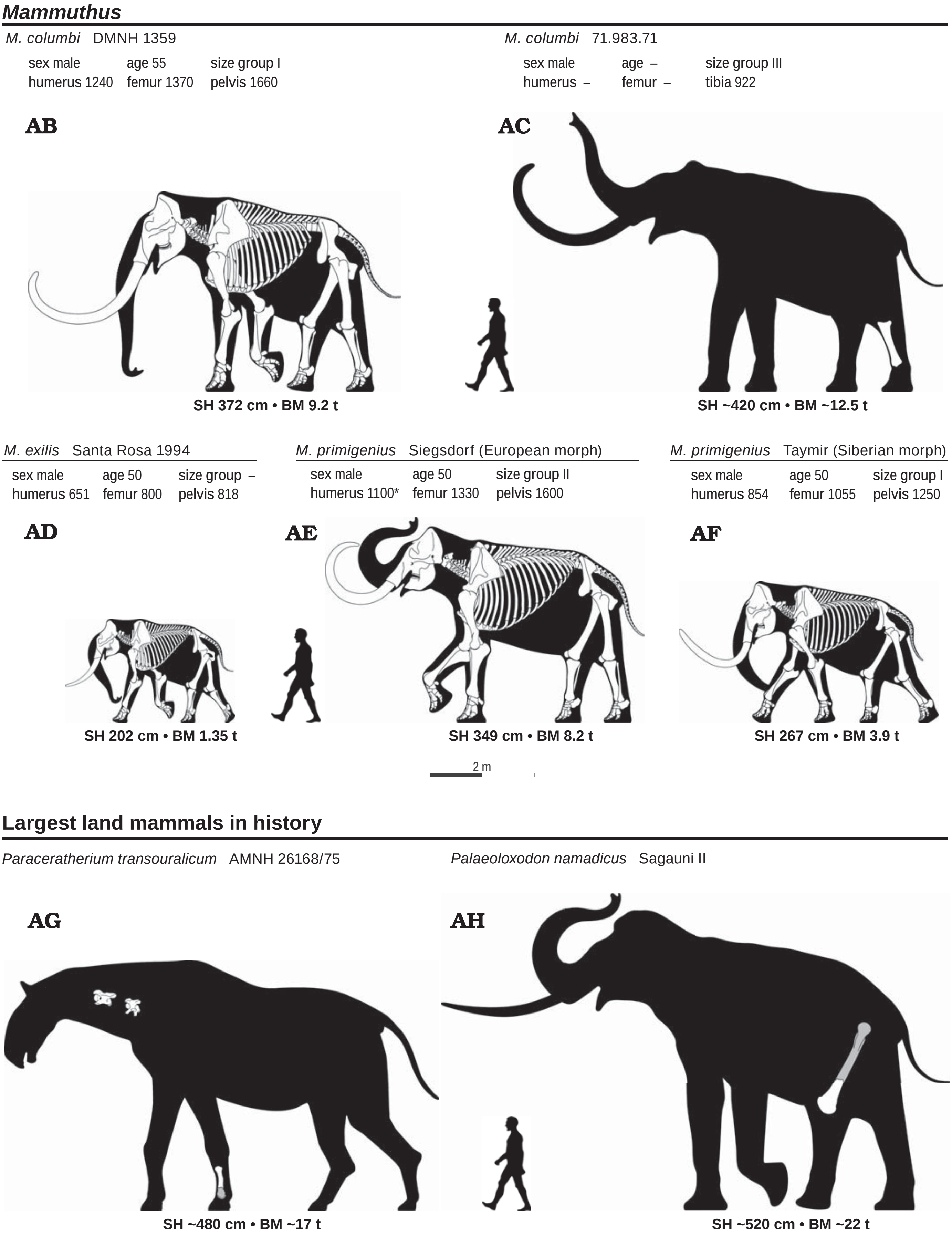


SH 359 cm • BM 10.3 t


Deinotherium
D. “thraceiensis” Ezerovo
sex male
age 45
size group –
humerus 1146
femur 1650
pelvis 2020
G
SH 401 cm • BM 13.2 t
Mammut
M. borsoni Milia I and Milia V
sex male
age 40 and 30
size group I
humerus 1250
femur 1435e
pelvis –
H
SH 390 cm • BM ~14 t
2 m
Mammut
M. borsoni Milia II
sex male
age –
size group I
humerus –
femur 1500
pelvis –
I
SH ~410 cm • BM ~16 t
M. americanum AMNH 9950 (Warren)
sex male
age 35
size group I
humerus 950*
femur 1060
pelvis 1826
J
SH 289 cm • BM 7.8 t
Mammut
M. americanum 595BS71
sex male
age –
size group II
humerus –
femur 1216
pelvis –
K
SH ~325 cm • BM ~11 t
Gomphotherium
G. productum DMNH 1261
sex male
age 35
size group –
humerus 772*
femur 1022
pelvis 1465
L
SH 251 cm • BM 4.6 t
G. steinheimense Mühldorf
sex male
age 37
size group –
humerus 1010
femur 1230
pelvis 1550
M
SH 317 cm • BM 6.7 t


Stegomastodon
S. mirificus NMNH 10707
sex male age 30 size group –
humerus 850* femur 1010 pelvis 1475
N
SH 260 cm • BM 4.7 t
Notiomastodon
N. platensis MECN 82
sex male age 35 size group –
humerus 866 femur 965 pelvis 1500
O
SH 252 cm • BM 4.4 t
Sinomastodon
S. hanjiangensis SBV 8006
sex ? age 30 size group –
humerus 680 femur 790 pelvis 980
P
SH 207 cm • BM 2.1 t
Stegodon
S. zdanskyi Yellow river
sex male age >50 size group –
humerus 1210 femur 1460 pelvis 2000
Q
SH 387 cm • BM 12.7 t
Loxodonta
L. africana AMNH 3283 (Jumbo)
sex male age 24 size group I–II
humerus 1091 femur 1258 pelvis 1340
R
SH 323 cm • BM 6.15 t
Elephas
E. maximus A. 1225
sex male age 18 size group –
humerus 830 femur 1000 pelvis 1150
S
SH 253 cm • BM 3.1 t
2 m
Palaeoloxodon
P. recki Koobi Fora
sex male age 40 size group –
humerus 1400 femur 1580 pelvis –
T
SH 427 cm • BM 12.3 t
P. namadicus Sagauni I
sex male age young adult size group –
humerus 1450 femur 1600 pelvis –
U
SH 435e cm • BM ~13 t


Palaeoloxodon
P. antiquus Viterbo
sex male? age 40 size group I
humerus 1230* femur 1440 pelvis 1810
V
SH 381 cm • BM 11.3 t
P. antiquus Montreuil
sex male age >50 size group I–II
humerus 1350* femur – pelvis –
W
SH 420e cm • BM ~15 t
2 m
Mammuthus
M. subplanifrons KNM KP-385 and KNM KP-397
sex male? age 50 size group –
humerus 1162* femur 1360 pelvis –
X
SH 368 cm • BM ~9 t
M. meridionalis Scoppito
sex male age 55 size group I
humerus 1320 femur 1455 pelvis 1750
Y
SH 397 cm • BM 10.7 t
M. trogontherii Zhalainuoer III
sex male age 52 size group I
humerus 1274 femur 1415 pelvis 1800
Z
SH 389 cm • BM 10.4 t
M. trogontherii MNHM PW1947/23 (Mosbach)
sex male age > 50 size group III
humerus 1463 femur – pelvis 1830
AA
SH 450e cm • BM ~14.3 t


Mammuthus
M. columbi DMNH 1359
sex male
age 55
size group I
humerus 1240
femur 1370
pelvis 1660
AB
SH 372 cm • BM 9.2 t
M. columbi 71.983.71
sex male
age –
size group III
humerus –
femur –
tibia 922
AC
SH ~420 cm • BM ~12.5 t
M. exilis Santa Rosa 1994
sex male
age 50
size group –
humerus 651
femur 800
pelvis 818
AD
SH 202 cm • BM 1.35 t
M. primigenius Siegsdorf (European morph)
sex male
age 50
size group II
humerus 1100*
femur 1330
pelvis 1600
AE
SH 349 cm • BM 8.2 t
M. primigenius Taymir (Siberian morph)
sex male
age 50
size group I
humerus 854
femur 1055
pelvis 1250
AF
SH 267 cm • BM 3.9 t
2 m
Largest land mammals in history
Paraceratherium transouralicum AMNH 26168/75
AG
SH ~480 cm • BM ~17 t
Palaeoloxodon namadicus Sagauni II
AH
SH ~520 cm • BM ~22 t