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Body size in proboscideans, with notes on elephant metabolism

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Mass estimates for a number of fossil proboscideans were computed using regression analyses on appendicular bones to body mass, for seven specimens of modern elephants, for which body masses had been recorded prior to death. The marked differences in physical proportions between extant *Loxodonta* and *Elephas*, implying substantial differences in body mass at any given shoulder height, were not present in their long bone parameters. Length and least circumferences proved to be the best parameters for prediction of body mass. Some extinct proboscideans, notably certain *Mammuthus* and *Deinotherium*, were much larger than extant elephants. Both the basal and the field metabolic rates of extant elephants are lower than predicted for a hypothetical mammal, in accordance with their body size and subsistence on low-quality foods. The feeding quantities often ascribed to extant wild elephants are exaggerated, and would in fact have sufficed to nourish much larger species.

ADDITIONAL KEYWORDS: body mass – limb bones – mammoths.

INTRODUCTION

With the possible exception of the giant indricothere rhinoceroses from the Oligocene of Asia (Granger & Gregory, 1936; Alexander, 1989; Fortelius & Kappelman, 1993; Paul, 1997) the Proboscidea encompasses the largest land mammals in history. Today the group is represented by what is probably the lowest diversity since its time of origin in the Palaeocene (Gheerbrant, Sudre & Capetta, 1996; see also Novacek, 1992; Archibald, 1996; Hedges *et al*., 1996). A rough estimation of the size span throughout the phylogenetic and temporal history of the Proboscidea reveals that extant elephants appear to be among the larger forms, although, based on linear dimensions of bones, significantly larger species once appear to have existed. Being the largest representatives in the ecosystems across most of the globe throughout much of the Tertiary, it is of some significance to have an assessment of the actual mass of proboscideans, because many physiological and ecological variables are related to body mass, including metabolic rate, food consumption, gestation time, territorial size and forage area (e.g. Adolph, 1943; Kleiber, 1961; Fleming, 1973; Jarman, 1974; Millar, 1977, 1981; Harestad & Bunnell, 1979; McMahon & Bonner, 1983; Peters, 1983; Calder, 1984; Nagy, 1987; McNab, 1988, 1990; Brown & Maurer, 1989; Eisenberg, 1990; Maiorana, 1990; Schmidt-Nielsen, 1995).

When predicting the body mass of extinct animals it is preferable to restrict the reference database of extant species to forms of broadly similar physical proportions and, if possible, close phylogenetic relatedness (Hartwig-Scherer, 1993; Biknevicius, 1999; see also Damuth, 1990; Fortelius, 1990). These two criteria can be met for fossil proboscideans by the exclusive use of extant elephants for mass prediction and, in fact, no other extant animals share the physical proportions of proboscideans. Even so, extant elephants appear most similar in physical proportions to their close phylogenetic relatives within the Elephantidae, and progressing backwards throughout their evolutionary prehistory, more archaic proboscideans appear to become less and less similar to extant forms, being more low-slung, with proportionally longer backs,

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longer, more dorsoventrally compressed heads and often a more massive overall build, even in taxa bearing substantial overall similarity to extant elephants, such as *Mammut* (Warren, 1852; Osborn, 1936, 1942; Miller, 1987; Haynes, 1991; P. Christiansen, unpubl. data).

Among extant elephants there is a significant relationship between body mass and shoulder height (Laws, 1966; Hanks, 1972; Laws, Parker & Johnstone, 1975; Roth, 1990; see also below), which appears even closer when combined with other physical proportions such as body length or thorax girth (Kurt & Hartl, 1995; Kurt & Kumarasinghe, 1998; see also Hile, Hintz & Erb, 1997). Significant relationships between body mass and tusk size and adrenal weight (Hanks, 1972; Sukumar, Joshi & Krishnamurthy, 1988) and between body mass and hind limb mass have been found (Laws, Parker & Archer, 1967; see also Robertson-Bullock, 1962). Shoulder heights are, however, less satisfactory for use in prediction of mass for the present purpose, in part owing to differences in physical stature of extant elephants from more archaic proboscideans, as noted above, and in part owing to substantial physical differences between the two extant species (Osborn, 1942; Robertson-Bullock, 1962; Shoshani *et al*., 1991; Shoshani, 1995), resulting in an often markedly greater body mass of *Elephas* compared with *Loxodonta* at any given shoulder height (Roth, 1990; see also Hanks, 1972). This would argue in favour of using osteometric variables for prediction of body mass in extinct proboscideans.

Frequently used in mass estimation of mammals are dental parameters (e.g. Gingerich, 1976, 1977; Gingerich, Smith & Rosenberg, 1982; Legendre & Roth, 1988; Damuth, 1990; Fortelius, 1990; Janis, 1990; see also Gould, 1975; Creighton, 1980). Limb bones appear to be superior to craniodental variables in terms of predictive reliability (e.g. Damuth & MacFadden, 1990; Damuth, 1990; Fortelius, 1990; Gingerich, 1990; Dagosto & Terranova, 1992; Anyonge, 1993; Biknevicius, 1999; see also Christiansen, 1999a, 2002), but are also preferable from the logical point of view of support of mass under the influence of gravity being carried out by the appendicular anatomy, not the cranium (Hylander, 1985). For proboscideans, the apomorphic dental anatomy and replacement pattern of elephantids compared with the more primitive dental morphology and replacement pattern in 'gomphotheres', mastodonts (*s.s.*), deinotheres and the plesiomorphic outgroups to Deinotheriidae + Elephantiformes (Tassy, 1995a, b) urges for caution in using the teeth of extant elephants for mass prediction (see also Roth, 1990), even in many of their fossil relatives with an overall similar postcranial anatomy such as *Mammut*, and even the low-crowned and otherwise very elephantid-like *Stegodon*.

The appendicular anatomy of virtually all proboscideans, with the exception of the most archaic, e.g. *Moeritherium* and *Numidotherium* (Court, 1994, 1995), appears very similar, but is substantially different from those of other mammals. Thus, the apomorphic columnar stance, straight-limbed gait, favouring axially compressive and simple lateromedial bending forces over more complex bending and torsional secondary moments during locomotion, and inability to perform true running (Gambaryan, 1974; Alexander *et al*., 1979; Alexander, 1983; Langman *et al*., 1995; Christiansen, 1997; Carrano, 1998; Paul & Christiansen, 2001; Hutchinson *et al*., 2003) can be inferred to have been similar in most extinct proboscideans as well. Among all extant, parasagittal animals the safety factors of the limb bones appear highly constrained (Alexander, 1981; Biewener, 1989, 1990) probably owing to their importance in fitness (Alexander, 1981), implying that this would also have been the case among extinct forms (Alexander, 1989; Christiansen, 1997, 1998). The highly apomorphic appendicular anatomy and mode of locomotion would tend to invalidate comparison with other, flexed-limbed, running ungulates for the purpose of mass prediction (but see Roth, 1990), leaving only extant elephants available for prediction of mass in extinct proboscideans.

Accordingly, for this study a sample of extant elephants were used from which body masses were known. These animals had ended up in museum collections, which is unusual for weighed elephants. The employment of osteometric data from the two species of extant elephants is clearly preferable to any other kind of analyses for computation of mass in extinct proboscideans. It does, however, pose one problem that cannot be circumvented, namely the pooling of individual specimens of both species into a common database, thus confusing intra- and interspecific allometry.

MATERIAL AND METHODS

Seven extant elephants were measured for which body masses had been recorded prior to or immediately after death (Table 1). All were captive specimens, except ZE.1961.8.9.82, and thus weights were obtained by zoo staff and/or veterinaries just after death, except for *Elephas maximus* CN 3109 from Copenhagen Zoo. Here, the cows and young adults are weighed in public every April, and this animal, which died in October 1996, weighed 3298 kg in April that year, which is the mass used in this study (she weighed 3320 kg in April 1995). ZE.1961.8.9.82 was a wild *Loxodonta* cow, which was weighed in sections 16 h after death (see Ansell, 1960).

A total of 34 osteological variables were chosen from the major limb bones. Overall bone lengths (joint to

Table 1. Body mass (kg) and bone variables (mm) used in the analyses. All are log values

	Loxodonta africana			*Elephas maximus*			
	CN 3684	ROMV R6000	ZE.1961.8.9.82	NMR 98-184	CN 1399	CN 3109	CN 558
Body mass	3.7959	3.8085	3.4351	3.7482	3.5483	3.5183	2.9294
Humerus							
Length	3.0249	2.9917	2.9031	2.9948	2.9201	2.9042	2.6767
Least circ.	2.6170	2.6149	2.4654	2.5763	2.4942	2.4955	2.1847
Diap.ap.	2.1415	2.1492	1.9823	2.1021	2.0086	2.0000	1.7033
Diap.lm.	2.0969	2.0828	1.9542	2.0531	1.9868	1.9956	1.6721
Art.width	2.3598	2.3522	2.2430	2.3560	2.2625	2.2405	2.1492
Med.con.l.	2.1903	2.0719	1.9912	2.1430	2.1239	2.0934	1.8808
Med.con.w.	2.0492	2.0792	1.9912	2.0294	1.9590	1.9243	1.8129
Lat.con.l.	2.1553	2.0531	1.9542	2.1172	2.1004	2.0170	1.8451
Lat.con.w.	1.9823	2.0170	1.8865	2.0492	1.9494	1.8389	1.8573
Radius							
Length	2.9101	2.8960	2.7959	2.8876	2.8089	2.8176	2.5682
Least circ.	2.3160	2.2810	2.1399	2.1959	2.1173	2.1303	1.8451
Diap.ap.	1.9085	1.7745	1.6435	1.8261	1.6435	1.6857	1.3892
Diap.lm.	1.7033	1.7924	1.6385	1.5185	1.5966	1.5740	1.3118
Ulna							
Length	2.9704	2.9504	2.8488	2.9479	2.8800	2.8669	2.6335
Least circ.	2.5340	2.5587	2.3802	2.5302	2.4100	2.3962	2.1173
Diap.ap.	2.0128	2.0792	1.8780	2.0000	1.8692	1.8976	1.6721
Diap.lm.	2.0588	2.0453	1.8893	2.0645	1.9518	1.9004	1.5623
Femur							
Length	3.0689	3.0881	3.0037	3.0700	2.9983	2.9814	2.7924
Least circ.	2.5866	2.6000	2.4330	2.5441	2.5119	2.5302	2.1703
Diap.ap.	2.0000	2.0531	1.8633	1.9912	1.9445	1.9567	1.6532
Diap.lm.	2.1644	2.1461	1.9956	2.0969	2.0755	2.0986	1.6946
Art.width	2.3404	2.3304	2.2648	2.3202	2.2068	2.2041	2.1004
Med.con.l.	2.1818	2.0969	1.9638	2.0934	2.0170	2.0645	2.0000
Med.con.w.	2.0531	2.0569	1.9494	2.0294	1.8808	1.9031	1.7324
Lat.con.l.	2.0755	1.9912	1.8808	1.9912	1.9542	1.9494	1.8692
Lat.con.w.	1.9912	1.9542	1.8195	1.9731	1.8633	1.8633	1.6628
Tibia							
Length	2.8871	2.8825	2.7745	2.8525	2.7825	2.7505	2.5119
Least circ.	2.4579	2.4564	2.3243	2.4771	2.3598	2.3503	2.1430
Diap.ap.	1.9370	1.9085	1.7818	1.9445	1.8325	1.8096	2.3118
Diap.lm.	1.9845	2.0043	1.8692	2.0128	1.8921	1.8921	1.3802
Fibula							
Length	2.8116	2.8370	2.7482	2.8325	2.7218	2.7356	2.4698
Least circ.	2.0334	2.0212	1.8692	2.0414	1.9138	1.9294	1.6232
Diap.ap.	1.6181	1.5623	1.4549	1.6385	1.5185	1.5052	0.9294
Diap.lm.	1.4314	1.3118	1.2672	1.4314	1.2788	1.3424	0.6990

joint) and diaphysial least circumferences were measured with a measuring tape. All other measurements were taken with calipers. Raw values were log transformed and bivariate regression analyses were fitted to the data by means of a Model II Reduced Major Axis (RMA) analysis with body mass as the 'dependent' variable. Regardless of the assigning of dependence to one variable (body mass) a Model II analysis is appropriate because error must be assumed on both variables (Labarbera, 1989; Sokal & Rohlf, 1995). Confidence limits (95% CI) were computed for both regression constants (coefficient and exponent) and the F statistic was also computed for each regression. Additionally, the significance of the variables was evaluated with a t-test (two-tailed P).

Multiple regression analyses were also performed on the variables, and regression statistics were computed for each analysis as above. However, a t-test (two-tailed P) performed on the variables was used to evaluate variable redundancy. A regression analysis with one (or more) slope variables with a $P \geq 0.1$ was discarded owing to variable redundancy. Thirty-four osteological variables potentially implies a very large number of multiple regression analyses, but few did, in fact, survive the test of variable redundancy, owing to the often very high correlation coefficients between most osteological variables and body mass in the bivariate analyses, as noted below.

Most frequently the correlation between two or more regression variables is evaluated by means of the correlation coefficient (r, e.g. Sokal & Rohlf, 1995). This is, however, not a satisfactory criterion for evaluation of the true goodness of fit of the data and the predictive reliability of an equation, because a large data sample with a slope far from zero can often imply a high correlation coefficient regardless of high residuals (e.g. Smith, 1981, 1984). Thus, it has become commonplace to regard the per cent standard error of the estimate (%SEE) and the per cent prediction error (%PE) as superior to the correlation coefficient in evaluating the predictive power of a regression equation. The standard error of the estimate provides an evaluation of the spread in accuracy of the predicted values, as 68% of the actual mass values would be expected to fall within ∀%SEE, assuming a normal distribution (see Van Valkenburgh, 1990). The %PE gives the average percentile difference between the actual and predicted values.

A number of fossil proboscideans were measured for the purpose of this and other previous studies (e.g. Christiansen, 1997, 1998; and unpubl. data). Most were isolated bones (Appendix 2), but others were represented by either several bones from a single individual or from a nearly complete, mounted skeleton (Appendix 1). The mounted skeleton from Brussels is, however, a composite. Measurements were taken as with the extant specimens. Because some specimens had been measured for the purpose of other studies, not all variables were present (e.g. condyle morphology) in all cases, but as noted below the length and diaphysial proportions emerged as the most reliable predictors of mass and these were always available.

For comparative purposes only the masses of the included skeletal mounts (two *Mammuthus primigenius* and one *M. meridionalis*; see Appendix 1) were also computed using shoulder heights, and it was decided to use data from both *Elephas maximus* and *Loxodonta africana*. Benedict (1936) listed the heights and masses of a number of captive *Elephas maximus* cows, and these were supplemented with additional data from zoos (Table 2). For bulls, data from Wood (1981) were supplemented with additional data from zoos. Although obese specimens were excluded, all included specimens were nonetheless captive animals,

Table 2. Shoulder heights and actual body masses of Asian elephants (*Elephas maximus*)

Females		Males	
Shoulder height (cm)	Body mass (kg)	Shoulder height (cm)	Body mass (kg)
201[1]	1970	165[2]	992
203[1]	1810	269[3]	4912
203[1]	2060	275[5]	5100
211[1]	1720	294[6]	5440
211[1]	2060	301[6]	5000
211[1]	2220	304[6]	5443
213[1]	2020	309[6]	6198
213[1]	2070	309[6]	6492
213[1]	2250		
216[1]	2040		
216[1]	2040		
218[1]	2580		
221[1]	2070		
224[1]	2240		
224[1]	2430		
226[1]	3040		
226[1]	3130		
229[1]	2640		
229[1]	2660		
229[1]	3120		
230[2]	3028		
231[1]	2630		
231[1]	2910		
231[1]	2950		
232[2]	3122		
234[1]	2810		
234[1]	3030		
234[1]	3540		
236[1]	2680		
236[1]	3080		
239[1]	3010		
239[1]	3240		
239[1]	4160		
244[1]	4050		
246[1]	3672		
247[2]	4464		
249[1]	3570		
251[3]	4404		
252[4]	4767		

[1] Data from Benedict (1936).
[2] From Copenhagen Zoo, weighed april 1999, measured May 1999, courtesy of Jørgen Jensen and John Stegman.
[3] From Los Angeles Zoo, courtesy of curator Michael Dee.
[4] From Santa Barbara Zoo, courtesy of Brian Gisi.
[5] From Givskud Zoo, courtesy of Richard Osterballe.
[6] From Wood (1981).

and a slight inaccuracy could thus be introduced because of physical differences between captive and wild specimens (Sukumar *et al.*, 1988), but physical differences are also apparent between various races of at least the Asian elephant (Kurt & Kumarasinghe, 1998). For fossil species the possible bias cannot be evaluated.

The body masses of the three included *Mammuthus* skeletal mounts were also estimated using regression equations based on African elephants. Laws *et al.* (1975) computed the following for bulls from Uganda:

$$\text{Body mass (kg)} = 5.07 \times 10^{-4} \times \text{SH}^{2.803} \quad (1)$$

where SH is shoulder height in centimetres. Johnson & Buss (1965) computed a regression equation for Ugandan bulls with a slightly higher exponent and a slightly lower coefficient. Laws *et al.* (1975) also computed a regression equation for *Loxodonta* cows from Murchison falls:

$$\text{Body mass (kg)} = 1.267 \times 10^{-3} \times \text{SH}^{2.631} \quad (2)$$

Their equation for females from Uganda from Laws *et al.* (1975) had a lower coefficient and a higher exponent. Finally, Hanks (1972) computed a regression equation for *Loxodonta* cows from Zambia:

$$\text{Body mass (kg)} = 1.02 \times 10^{-4} \times \text{SH}^{3.11} \quad (3)$$

which had a very high correlation coefficient (0.992).

The skeletal mounts of *Mammuthus* would have been taller in life, owing to skin and subcutaneous tissue at the back and below the foot, and cartilage in the joints. The skin of an *Elephas maximus* cow was found to be 3.2 cm thick along the back (Shoshani *et al.*, 1982), and Roth (1990) used twice this value for the thickness of the sole of the foot. This resulted in an extra 10 cm to be added to the skeletal shoulder height for smaller species and 15 cm for large species, the latter figure which is repeated here, because the included specimens were large. Osborn (1942, e.g. p. 1022) added slightly more to the skeletal height. There does not, however, appear to be a substantial difference between the standing and lying shoulder height of extant elephants (Hanks, 1972; contra Wood, 1981).

RESULTS

The relationship between shoulder height and body mass in the *Elephas maximus* cows and bulls from Table 2 were evaluated with model II (reduced major axis) analyses, unlike eqns 1–3, which were normal model I (least squares) analyses. The following equations were obtained:

all specimens

$$\text{Log(BM[kg])} = -4.016 \pm 0.730 + 3.161 \pm 0.308\text{Log(SH[cm])} \quad (4)$$

($n = 48$; $r = 0.945$; $F = 380.688$ ($P < 0.000$); %SEE = 13.47; %PE = 10.32);

cows only

$$\text{Log (BM [kg])} = -6.731 \pm 1.432 + 4.316 \pm 0.608\text{Log (SH [cm])} \quad (5)$$

($n = 40$; $r = 0.903$; $F = 168.744$ ($P < 0.000$); %SEE = 12.09; %PE = 9.77);

bulls only

$$\text{Log (BM [kg])} = -3.436 \pm 1.196 + 2.906 \pm 0.491\text{Log (SH [cm])} \quad (6)$$

($n = 8$; $r = 0.986$; $F = 204.309$ ($P < 0.000$); %SEE = 11.83; %PE = 7.70).

Despite the higher correlation coefficient of the total sample compared with the sample of cows only, the latter is in fact superior in prediction of mass, at least in *Elephas maximus*, owing to the lower %SEE and %PE, a reflection of the differences in physical proportions and growth trajectories between bulls and cows (Sukumar *et al.*, 1988; Kurt & Kumarasinghe, 1998; see also Hanks, 1972; Lee & Moss, 1995). The higher correlation coefficient of the total sample can be regarded as a bias of higher sample size, as noted by Smith (1981, 1984). The sample of bulls only appears to be the best.

Although confusion of intra- and interspecific allometry should be avoided, the presence of a mere two species of extant elephants makes this unavoidable. It is thus fortunate that the differences in body mass and overall physical stature between *Elephas* and *Loxodonta* are not reflected in analyses regressing body mass to the osteometric variables used in this study. This corroborates the rationale for relying primarily on osteometric variables for prediction of mass, as outlined above.

Rather, all length parameters (Tables 3 and 4; see also Figs 1A, D, 2A, D) displayed high correlation coefficients and low %SEEs and %PEs. As can be seen from both the high correlation coefficients and low %SEEs and %PEs, and also from the plots (Figs 1, 2), extant elephants appear considerably homogeneous with regard to long bone proportions, because the specimens fall virtually on the regression lines. By contrast, body mass to shoulder height comparisons result in much wider scatter if the two species are pooled (e.g. Hanks, 1972; Roth, 1990; see also Haynes, 1991). Least circumference also yielded low %SEE and %PE values (Tables 3, 4; Figs 1B, F, 2E, F), corroborating previous studies on other mammals (Ruff, 1990; Anyonge, 1993; Biknevicius, 1999; Christiansen, 1999b). Diaphysial diameters yielded slightly higher %SEE and %PE values than least circumference for the epipodial bones (Tables 3, 4; Figs 1C, 2B) but diaphysial anteroposterior diameter was superior to least circumference for the propodial bones.

Table 3. Body mass and forelimb parameters in *Elephas maximus* and *Loxodonta africana*. Equations are of the form log(mass in kg) = a + b(log X), where X are bone variables (mm)

Variable	a ± 95% CI	P	b ± 95% CI	P	F	P	r	%SEE	%PE
Humerus length	–4.145 ± 1.250	0.000	2.635 ± 0.428	0.000	246.97	0.000	0.990	11.52	6.74
Humerus circ.	–1.598 ± 0.574	0.001	2.062 ± 0.230	0.000	529.34	0.000	0.995	7.78	5.54
Humerus diap.ap	–0.503 ± 1.107	0.015	2.009 ± 0.173	0.000	885.43	0.000	0.997	5.97	3.62
Humerus diap.lm	–0.660 ± 0.720	0.080	2.124 ± 0.363	0.000	220.74	0.000	0.989	12.21	8.56
Humerus dist.art	–5.290 ± 3.180	0.007	3.872 ± 1.252	0.001	58.18	0.001	0.960	24.33	16.72
Humerus mcl	–2.554 ± 3.250	0.201	2.943 ± 1.568	0.008	18.30	0.008	0.881	43.15	28.34
Humerus mcw	–3.202 ± 2.560	0.036	3.409 ± 1.293	0.001	40.97	0.001	0.944	29.09	18.51
Humerus lcl	–2.294 ± 2.878	0.183	2.867 ± 1.413	0.005	22.23	0.005	0.904	39.34	25.43
Humerus lcw	–3.784 ± 5.545	0.404	3.775 ± 2.861	0.051	6.51	0.051	0.752	66.58	39.61
Radius length	–3.838 ± 1.052	0.000	2.634 ± 0.374	0.000	318.01	0.000	0.992	10.11	6.64
Radius circ.	–0.754 ± 1.167	0.222	2.001 ± 0.543	0.000	84.86	0.000	0.972	20.04	12.30
Radius diap.ap	–0.430 ± 1.032	0.221	1.834 ± 0.606	0.001	55.57	0.001	0.958	24.91	15.31
Radius diap.lm	–0.332 ± 2.045	0.326	2.017 ± 1.281	0.020	11.39	0.020	0.834	53.36	30.14
Radius diap.lm*	–0.351 ± 1.231	0.343	1.969 ± 0.765	0.002	47.10	0.002	0.960	26.01	16.30
Ulna length	–4.135 ± 0.927	0.000	2.674 ± 0.323	0.000	454.19	0.000	0.995	8.41	5.34
Ulna circ.	–1.349 ± 0.407	0.000	2.022 ± 0.168	0.000	944.92	0.000	0.997	5.78	4.42
Ulna diap.ap	–0.872 ± 1.151	0.151	2.304 ± 0.600	0.000	92.55	0.000	0.974	19.16	11.79
Ulna diap.lm	–0.185 ± 0.497	0.322	1.743 ± 0.257	0.000	296.73	0.000	0.992	10.48	7.88

*Excluding NMR 98-184.

Abbreviations: circ., least circumference of diaphysis; diap.ap, diaphysial diameter in the anteroposterior plane; diap.lm, diaphysial diameter in the lateromedial plane; dist.art, width of distal articular surface; lcl, lateral condyle length; lcw, lateral condyle width; mcl, medial condyle length; mcw, medial condyle width.

Table 4. Body mass and hindlimb parameters in *Elephas maximus* and *Loxodonta africana*. Equations are of the form log(mass in kg) = a + b(log X), where X are bone variables (mm). Abbreviations per Table 3

Variable	a ± 95% CI	P	b ± 95% CI	P	F	P	r	%SEE	%PE
Femur length	–5.568 ± 1.844	0.001	3.036 ± 0.614	0.000	157.65	0.000	0.985	14.54	6.15
Femur circ.	–1.606 ± 1.296	0.032	2.073 ± 0.521	0.000	99.39	0.000	0.976	18.46	11.52
Femur diap.ap	–0.912 ± 1.020	0.093	2.315 ± 0.529	0.003	121.54	0.003	0.980	16.64	11.40
Femur diap.lm	–0.342 ± 1.160	0.663	1.904 ± 0.568	0.000	69.38	0.000	0.966	22.23	14.42
Femur dist.art	–4.347 ± 3.386	0.035	3.502 ± 1.532	0.003	30.92	0.003	0.928	33.49	21.71
Femur mcl	–5.108 ± 7.097	0.403	4.199 ± 2.442	0.079	4.83	0.079	0.701	73.72	44.00
Femur mcl*	–0.819 ± 3.145	0.868	2.156 ± 1.519	0.027	11.53	0.027	0.862	23.42	15.35
Femur mcw	–1.550 ± 1.832	0.129	2.619 ± 0.942	0.001	46.15	0.001	0.950	27.39	17.71
Femur lcl	–4.970 ± 5.417	0.153	4.345 ± 2.764	0.020	11.33	0.020	0.833	53.49	30.98
Femur lcw	–1.514 ± 0.933	0.010	2.695 ± 0.497	0.000	189.56	0.000	0.987	13.21	9.91
Tibia length	–3.064 ± 1.154	0.001	2.378 ± 0.414	0.000	212.09	0.000	0.988	12.47	6.93
Tibia circ.	–2.724 ± 0.948	0.001	2.647 ± 0.400	0.000	283.94	0.000	0.991	10.72	6.57
Tibia diap.ap	–1.044 ± 0.663	0.008	1.395 ± 0.369	0.000	89.78	0.000	0.973	19.46	13.71
Tibia diap.lm	–0.950 ± 0.732	0.015	1.391 ± 0.390	0.000	78.80	0.000	0.970	20.82	14.12
Fibula length	–3.086 ± 1.687	0.007	2.422 ± 0.615	0.000	97.15	0.000	0.975	18.68	11.40
Fibula circ.	–0.483 ± 0.548	0.086	2.097 ± 0.284	0.000	354.04	0.000	0.993	9.57	6.24
Fibula diap.ap	–1.695 ± 0.610	0.001	1.263 ± 0.413	0.001	56.89	0.001	0.959	24.62	17.31
Fibula diap.lm	–2.020 ± 0.645	0.000	1.215 ± 0.507	0.002	33.08	0.002	0.932	32.38	19.97

*Excluding CN 558.

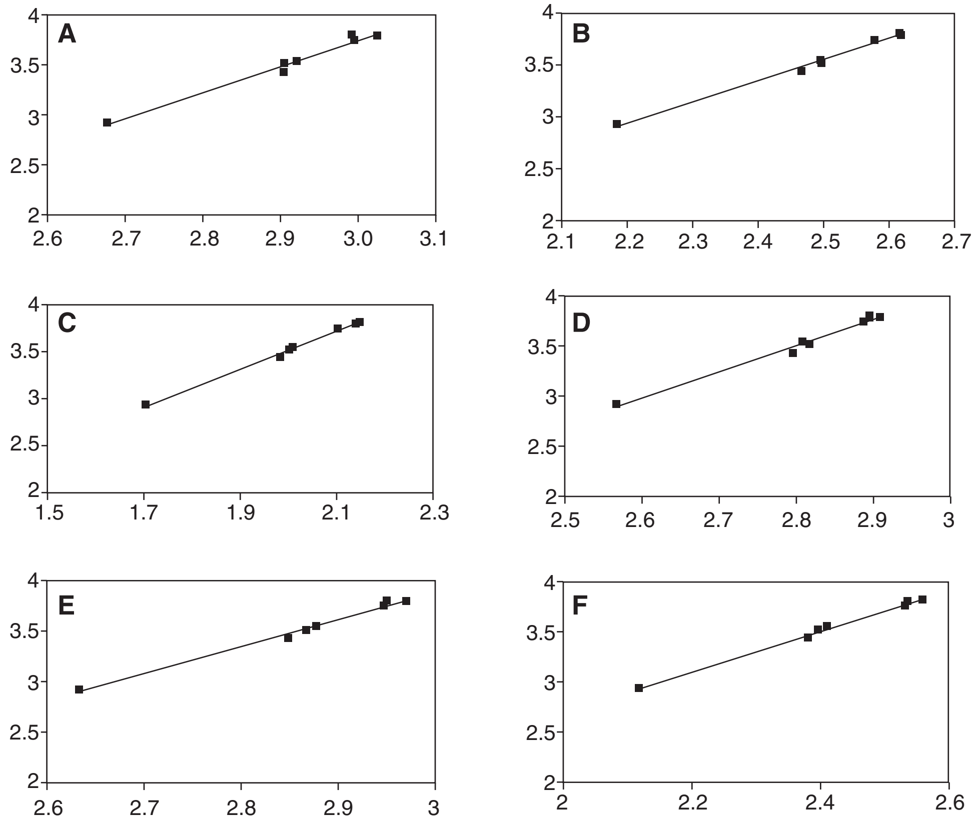

Figure 1. The best forelimb predictors of body mass in *Elephas maximus* and *Loxodonta africana*. The *y*-axis in all cases is log body mass. (A) Log humerus length; (B) log humerus least circumference; (C) log humerus diaphysis anteroposterior diameter; (D) log radius length; (E) log ulna length; (F) log ulna least circumference. For regression statistics see Table 3.

Based on the %SEE and %PE values, the five best osteological predictors of body mass were humerus anteroposterior diameter, ulna least circumference, humerus least circumference, ulna length and fibula least circumference, despite the last of these not being a primary weight-bearing bone. For individual bones the two best predictors were diaphysial anteroposterior diameter and least circumference (humerus), length and least circumference (radius), least circumference and length (ulna, tibia and fibula), and length and diaphysial anteroposterior diameter (femur). Condylar dimensions and distal articular width (humerus and femur) proved to be considerably poorer predictors of body mass (Tables 3, 4). The multivariate analyses (Table 5) yielded high correlation coefficients and low %PEs and %SEEs, with correspondingly high predictive power. In all but four cases (HMCl+HMCw, HMCw+HLCl, FeDlm+FeAw, FeDlm+FeMCw) the multivariate regressions require a partial skeleton, as they are on two separate bones.

Using the regressions for predicting the mass of fossil proboscideans (Appendices 1 and 2) it is evident that some fossil proboscideans did not share the physical proportions of extant elephants, and this pattern follows the phylogenetic relationships. As noted above, more archaic (i.e. non-elephantid) proboscideans were more stoutly built, with longer bodies and proportionally shorter and thicker limb bones. Accordingly, for *Elephas* and *Mammuthus* there is usually no pronounced dichotomy between mass values predicted from lengths vs. diaphysial dimensions, whereas in more archaic taxa (*Gomphotherium*, *Amebelodon*, *Serbelodon*, *Cuvieronius*, *Eubelodon*, *Stegomastodon*, *Palaeomastodon* and, to a lesser extent, *Mammut*) the values predicted from bone lengths were usually considerably below values predicted from diaphysial dimensions. This was, however, not the case in *Deinotherium* (Appendix 2).

Mammuthus primigenius appears to have been comparable in size to extant elephants (Tables 6, 7), although some specimens appear to have been particularly large (see also Osborn, 1942). *Mammuthus meridionalis*, *M. columbi* and *M. imperator* appear to have been somewhat larger than extant elephants, although not as large as their shoulder heights would suggest. This becomes evident when comparing the values predicted from bone dimensions with the val-

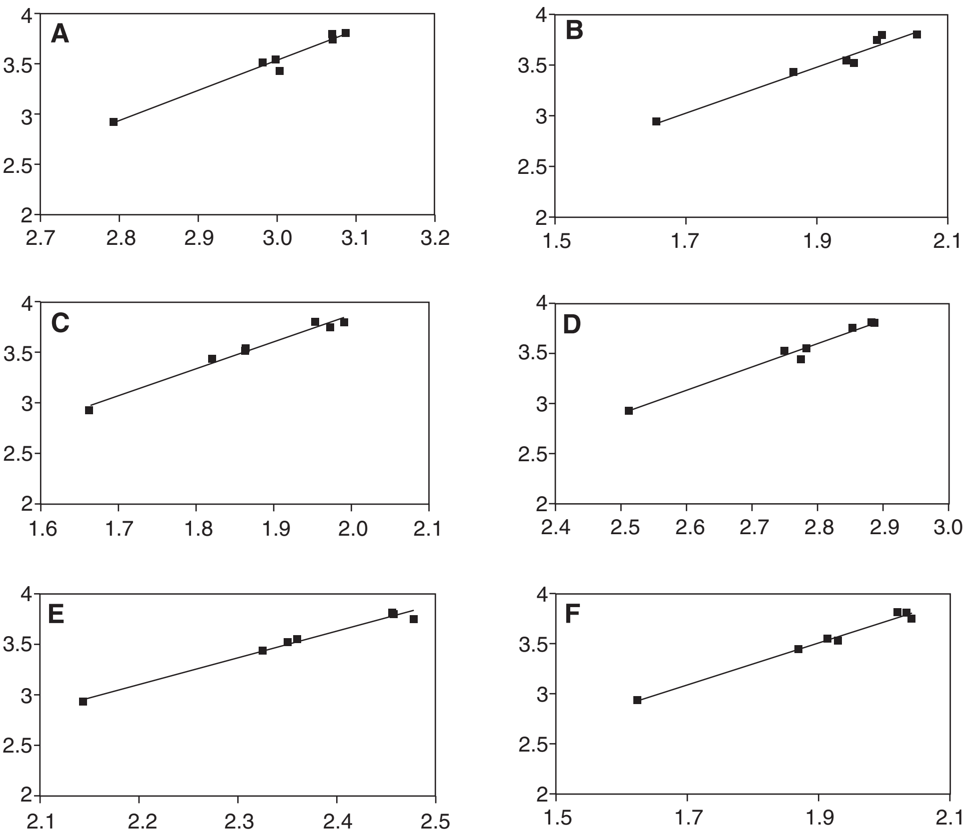

Figure 2. The best hindlimb predictors of body mass in *Elephas maximus* and *Loxodonta africana*. The *y*-axis in all cases is log body mass. (A) Log femur length; (B) log femur diaphysial anteroposterior diameter; (C) log femur lateral condyle width; (D) log tibia length; (E) log tibia least circumference; (F) log fibula least circumference. For regression statistics see Table 4.

ues predicted from eqns 1–6, and it is evident that eqn 5 results in mass values very much greater than predicted by the other equations, in accordance with findings that elephant cows invest more in body mass than height compared with bulls (Sukumar *et al.*, 1988; Kurt & Kumarasinghe, 1998). The included *Mammuthus* skeletons were all bulls.

Using the above equations, the Hebior Mammoth (Appendix 1; see also Kramer *et al.*, 1996) is predicted to have had a shoulder height in the flesh of 333 cm, resulting in a predicted body mass of 5692 kg (eqn 1), 5487 kg (eqn 2), 7135 kg (eqn 3), 9032 kg (eqn 4), 14 282 kg (eqn 5) and 7846 kg (eqn 6), but it is predicted to have weighed between 3900 and 6900 kg based on bone dimensions (Appendix 1, Table 6). A mounted skeleton of a bull in Brussels is predicted to have had a shoulder height of 340 cm, and is predicted to have weighed 6320 kg (eqn 1), 5796 kg (eqn 2), 7612 kg (eqn 3), 9464 kg (eqn 4), 15 624 kg (eqn 5) and 8335 kg (eqn 6), whereas the mass values based on osteometry usually are of the order of 6000–8000 kg, although the fibula appears to have been particularly slender in this animal and the humerus rather massive (Appendix 1, Table 6). The giant *M. meridionalis* in Paris is predicted to have had a shoulder height of 398 cm, and a mass of 9828 kg (eqn 1), 8771 kg (eqn 2), 12 424 kg (eqn 3), 15 868 kg (eqn 4), 30 833 kg (eqn 5) and 13 173 kg (eqn 6). The osteometric values (Appendix 1, Table 6) indicate a body mass of 7000–10 000 kg. This indicates that mammoths were taller, but proportionally less massive than extant *Elephas*, more resembling extant *Loxodonta* in being more long-limbed, and probably also with a proportionally shorter body than both species of extant elephants.

Elephas antiquus and *E. recki* appear to have been considerably larger species than *E. maximus* (Appendix 2, Table 7). *Mammut americanum* appears to have been somewhat heavier than both extant *Elephas* and *Loxodonta*, although no taller (Warren, 1852; Osborn, 1936, 1942) and specimens appear to have varied between 4000 and 8000 kg in body mass (Tables 6, 7). *Archaeobelodon*, *Cuvieronius*, *Amebelodon* and *Gomphotherium* were smaller than extant elephants, whereas *Stegomastodon* and *Serbelodon* appear to have been comparable with extant elephants in body

Table 5. Multivariate analyses on fore and hind limb parameters to body mass in *Elephas maximus* and *Loxodonta africana*. Equations are of the form log(mass in kg) = $a + b_1(\log X_1) + b_2(\log X_2)$, where X are bone variables (mm)

a ± 95% CI	P	Var (b_1)	b_1 ± 95% CI	P	Var (b_2)	b_2 ± 95% CI	P	F	P	r	%SEE	%PE
–2.938 ± 0.760	0.000	HAw	1.922 ± 0.503	0.000	FeDlm	1.028 ± 0.247	0.000	864.61	0.000	0.999	4.23	2.49
–1.655 ± 0.669	0.002	HMCl	0.981 ± 0.505	0.006	Udap	1.652 ± 0.396	0.000	320.88	0.000	0.997	7.15	4.45
–1.567 ± 0.665	0.003	HLCl	1.001 ± 0.538	0.007	Udap	1.603 ± 0.433	0.001	296.75	0.000	0.997	7.40	4.99
–3.996 ± 1.152	0.001	FeLCl	1.228 ± 0.832	0.015	Fil	1.875 ± 0.463	0.000	210.61	0.000	0.995	8.64	5.41
0.021 ± 0.835	0.948	UDap	1.181 ± 0.818	0.016	Tdap	0.702 ± 0.495	0.017	188.22	0.000	0.995	9.40	5.27
–2.047 ± 2.031	0.049	HAw	1.819 ± 1.181	0.013	TDlm	0.773 ± 0.425	0.007	184.79	0.000	0.995	9.40	5.78
0.162 ± 0.928	0.653	UDap	1.339 ± 0.739	0.007	FiDap	0.557 ± 0.405	0.019	179.53	0.000	0.994	9.40	5.68
–1.843 ± 2.252	0.000	HAw	1.732 ± 1.301	0.021	Tdap	0.801 ± 0.469	0.009	165.48	0.000	0.994	9.90	5.50
–0.783 ± 1.556	0.235	FeMCl	1.049 ± 0.863	0.028	TDlm	1.161 ± 0.285	0.000	126.91	0.000	0.992	11.43	6.10
–1.964 ± 2.504	0.095	HAw	2.001 ± 1.331	0.014	FiDap	0.644 ± 0.434	0.015	130.64	0.000	0.992	11.17	6.28
–0.951 ± 1.697	0.195	FeLCl	1.287 ± 1.064	0.028	TDlm	1.058 ± 0.340	0.001	126.08	0.000	0.992	11.43	6.49
–0.695 ± 0.748	0.061	UDap	1.275 ± 0.938	0.020	FeDap	0.879 ± 0.776	0.035	133.62	0.000	0.993	11.17	7.05
0.067 ± 1.129	0.877	UDap	1.525 ± 0.811	0.006	FiDlm	0.441 ± 0.428	0.046	116.93	0.000	0.992	11.94	6.50
–3.982 ± 1.614	0.002	FeMCl	0.911 ± 0.925	0.052	Fil	2.063 ± 0.533	0.000	115.30	0.000	0.991	11.94	6.98
–1.680 ± 1.494	0.035	HMCw	1.478 ± 1.299	0.034	FeDap	1.127 ± 0.725	0.012	102.00	0.000	0.990	12.72	6.26
–0.668 ± 1.894	0.383	TDap	5.195 ± 3.964	0.022	FiDap	–3.483 ± 3.589	0.054	104.68	0.000	0.991	12.46	6.76
–0.049 ± 1.105	0.909	UDap	1.229 ± 1.132	0.039	TDlm	0.663 ± 0.684	0.055	107.65	0.000	0.991	12.46	7.36
–2.085 ± 1.695	0.027	FeDlm	1.200 ± 0.629	0.006	FeAw	1.412 ± 1.157	0.028	113.14	0.000	0.991	12.20	7.51
–0.982 ± 0.964	0.048	FeDlm	1.092 ± 0.714	0.013	FeMCw	1.181 ± 0.982	0.029	110.75	0.000	0.991	12.20	7.61
–3.366 ± 1.335	0.002	HMCl	1.267 ± 0.808	0.012	HMCw	2.166 ± 0.935	0.003	103.61	0.000	0.990	12.72	7.78
–3.025 ± 1.310	0.003	HLCl	0.871 ± 1.008	0.074	Fil	1.751 ± 0.852	0.005	97.63	0.000	0.990	12.98	7.74
–0.435 ± 1.882	0.555	FeMCl	0.899 ± 1.052	0.077	TDap	1.187 ± 0.350	0.001	89.30	0.000	0.989	13.76	6.98
–2.404 ± 2.783	0.074	HAw	2.317 ± 1.415	0.010	FiDlm	0.527 ± 0.444	0.030	91.92	0.000	0.989	13.58	8.47
–4.053 ± 1.976	0.005	HAw	1.590 ± 2.003	0.092	Fil	1.450 ± 1.253	0.032	88.50	0.000	0.989	13.76	8.48
–2.209 ± 1.485	0.012	HMCl	1.175 ± 1.019	0.033	FeMCw	1.706 ± 0.907	0.006	70.85	0.001	0.986	15.35	9.66
–2.077 ± 1.397	0.015	HLCl	1.196 ± 1.079	0.037	FeMCw	1.638 ± 0.986	0.010	66.88	0.001	0.985	15.88	10.43
–0.533 ± 2.720	0.616	HMCw	1.531 ± 1.781	0.075	FiDap	0.715 ± 0.660	0.040	58.03	0.001	0.983	17.22	8.03
0.146 ± 1.882	0.840	FeMCw	1.229 ± 1.380	0.069	FiDap	0.688 ± 0.665	0.045	60.62	0.001	0.984	16.68	8.48
–3.098 ± 1.725	0.008	HMCw	2.080 ± 1.356	0.013	HLCl	1.240 ± 1.140	0.039	58.30	0.001	0.983	16.95	9.82
–0.872 ± 2.857	0.444	HMCw	1.867 ± 1.760	0.042	FiDlm	0.576 ± 0.627	0.063	46.29	0.002	0.979	19.40	8.44
–3.938 ± 2.310	0.009	HMCl	1.321 ± 1.252	0.043	FeAw	2.106 ± 1.490	0.017	43.20	0.002	0.978	19.95	12.36
–1.137 ± 4.108	0.485	FeAw	1.726 ± 2.157	0.090	FiDlm	0.631 ± 0.749	0.079	32.03	0.003	0.970	23.31	11.02
–3.667 ± 2.481	0.015	HLCl	1.333 ± 1.411	0.059	FeAw	1.996 ± 1.722	0.032	37.09	0.003	0.974	21.62	13.23
–1.538 ± 2.072	0.108	HLCl	1.800 ± 1.296	0.018	RDlm	0.891 ± 0.912	0.053	28.91	0.004	0.967	24.74	13.49
–1.636 ± 2.330	0.123	HMCl	1.773 ± 1.404	0.025	RDap	0.947 ± 0.963	0.052	24.70	0.006	0.962	26.77	15.34
–2.556 ± 4.464	0.187	RDlm	1.052 ± 1.273	0.083	FeLCl	2.258 ± 2.742	0.084	13.12	0.017	0.932	37.09	18.06

Abbreviations: FeAw, femur distal articular surface width; FeD, femur diaphysis; FeLC, femur lateral condyle; FiD, fibula diaphysis; Fil, fibula length; HAw, humerus distal articular surface width; HLC, humerus lateral condyle; HMC, humerus medial condyle; RD, radius diaphysis; TD, tibia diaphysis; UD, ulna diaphysis. In all cases ap and lm imply anteroposterior and lateromedial diameter, respectively, and l and w imply length and width, respectively.

mass (Tables 6, 7). *Palaeomastodon* (Table 7) was considerably smaller than extant elephants. *Deinotherium giganteum* was, by contrast, among the largest of the proboscideans, and large specimens appear to have weighed around 15 000 kg (Table 7).

DISCUSSION

The present analysis indicates that a simple comparison of shoulder heights among various proboscideans is unlikely to produce reliable results, and that osteometric variables, particularly the lengths and diaphysial proportions of the major long bones, are better at predicting body masses in proboscideans, as in other mammals. A mass evaluation based on shoulder heights is best restricted to phylogenetically and morphologically closely related species, i.e. the Elephantidae. Osborn (1942) stated shoulder heights of a number of mounted *Mammuthus* skeletons.

A medium-sized *M. meridionalis* had a skeletal shoulder height of 345 cm, indicating a shoulder height in the flesh of 360 cm. This animal is predicted

Table 6. Estimated body masses of extinct proboscideans, complete or partial skeletons. The two best equations for fore and hind limb, respectively, were chosen on the basis of the %SEE and %PE. The values for each individual are is the average values based on multiple regression equations, see Appendix 1 for details and Tables 3 and 4 for statistical parameters. All values are in kilograms

	Forelimb					Hindlimb				
			Average					Average		
Taxon	Best*	2nd best*	Humerus	Radius	Ulna	Best*	2nd best*	Femur	Tibia	Fibula
Mammuthus primigenius	3897	4297	5724	5133	4484	4413	6852	6848	5749	4823
Mammuthus primigenius	6170	6350	10917	4585	6647	3052	8801	7626	7052	4399
Mammuthus primigenius	3344	5076	3785	3527	4394	4513	4794	4301	4356	4466
Mammuthus primigenius	5050	–	5971	–	–	–	7599	5168	6088	–
Mammuthus primigenius	–	5240	–	–	4782	–	–	6393	–	–
Mammuthus meridionalis	6724	8384	9319	6412	8651	6639	10369	8446	8187	7042
Mammuthus meridionalis	8009	7528	7738	7143	7372	–	–	–	–	–
Mammuthus imperator	8640	–	9575	–	–	–	9093	9063	7978	–
Mammuthus imperator	5215	5474	7074	–	5412	–	7096	5867	6057	–
Mammuthus imperator	7652	8808	9143	8967	8842	–	–	–	–	–
Mammuthus imperator	5724	–	7613	–	–	–	–	7289	–	–
Mammut americanum	6915	7022	6592	–	6466	–	8601	8309	6735	–
Mammut americanum	7156	–	6457	–	–	–	8953	–	6457	–
Mammut americanum	–	7176	–	4599	6577	–	8953	–	6911	–
Mammut americanum	–	–	–	–	–	–	5343	3600	4589	–
Archaeobelodon filholi	2957	2509	3477	–	2350	–	–	–	–	–
Gomphotherium angustidens	3969	3290	3980	2957	3052	–	4104	3296	3974	–
Gomphotherium productum	–	2960	–	–	2952	–	1889	–	2616	–
Gomphotherium productum	–	4694	–	–	4677	–	4746	–	4685	–
Cuvieronius hyodon	3083	3638	4740	2972	3361	9343	9313	6336	6680	6274
Eubelodon morrilli	5510	5440	6046	–	5465	–	–	–	–	–
Stegomastodon platensis	6035	–	6103	–	–	–	–	4336	–	–

*The best predictive equations for the fore and hind limb were humerus diaphysis anteroposterior diameter and fibula circumference, respectively, and the 2nd best were ulna circumference and tibia circumference, respectively.

to have weighed between 6736 kg (eqn 2) and 19 996 kg (eqn 5) but, as noted above, the equations for African elephants (eqns 1–3) and, to some extent, the equation for Asian elephant bulls only (eqn 6) appear to be more appropriate for mammoths. Accordingly, this specimen had a body mass of 7000–9000 kg. Two *M. imperator* specimens had shoulder heights in the flesh of 370 and 407 cm, respectively, and are predicted to have weighed 8011 and 10 464 kg (eqn 1), 7240 and 9303 kg (eqn 2), 9902 and 13 318 kg (eqn 3) and 10 656 and 14 057 kg (eqn 6), respectively. One *M. imperator* specimen had a humerus of 1251 mm (Osborn, 1942), resulting in a predicted mass (Table 3) of around 10 400 kg, and another specimen had a humerus of 1270 mm, implying a mass of around 10 800 kg. Another specimen had a femur of 1422 mm, resulting in a predicted mass (Table 4) of around 10 100 kg.

In the present analysis, *Elephas recki* was found to be larger than extant elephants, with two specimens, perhaps cows (but this is unknown), having predicted masses of around 4 and 6 tons, whereas two other specimens, perhaps bulls, appear to have weighed around 9000 and 10 000–11 000 kg, respectively (Table 7). Osborn (1942) gave the skeletal shoulder height of one specimen as 360 cm (= around 375 cm in the flesh). This results in a predicted mass of 8318 kg (eqn 1), 7500 kg (eqn 2), 10 324 kg (eqn 3) and 11 080 kg (eqn 6). The same specimen had a humerus of 1235 mm and a femur of 1500 mm, resulting in predicted masses (Tables 3 and 4) of around 10 000 and 11 900 kg, respectively.

Elephas antiquus was also found to have been substantially larger than extant elephants (Table 7). In accordance with this, the *E. antiquus* specimen known as the Upnor elephant (Osborn, 1942) had a skeletal shoulder height of 370 cm (= around 385 cm in the flesh), resulting in a predicted body mass of 8955 (eqn 1), 8038 (eqn 2), 11204 (eqn 3) and 11 961 (eqn 6). One specimen of *E. antiquus* had a humerus of 1300 mm (Osborn, 1942), implying a body mass of around 11 500 kg, and another specimen had a femur

Table 7. Estimated body masses of extinct proboscideans, individual bones. The two best equations for the various bones were humerus diaphysis anteroposterior diameter and circumference, radius length and circumference, ulna circumference and length, femur length and diaphysis anteroposterior diameter and tibia circumference and length. These were chosen on the basis of the %SEE and %PE. See Appendix 2 for averages and Tables 3 and 4 for statistical parameters. All values are in kilograms

Taxon	Best	2nd best	Average	Taxon	Best	2nd best	Average
Humerus				**Femur**			
Elephas antiquus	4928	5308	5453	*Elephas recki*	3788	3445	3870
Elephas antiquus	8586	11897	11106	*Elephas recki*	5505	5986	6243
Elephas antiquus	5510	5777	5799	*Elephas recki*	8807	9601	9629
Elephas antiquus	4807	5511	5376	*Elephas recki*	11978	10299	10497
Elephas antiquus	9294	12335	13122	*Elephas antiquus*	4313	5475	5055
Mammuthus primigenius	9406	10146	10102	*Elephas antiquus*	5563	4476	6888
Mammuthus primigenius	2421	3544	3782	*Mammuthus primigenius*	7326	10932	9328
Mammuthus primigenius	3605	3591	3662	*Mammuthus primigenius*	3710	3738	4853
Mammuthus primigenius	2833	3303	3533	*Mammuthus primigenius*	3810	3941	4380
Mammuthus primigenius	3826	4943	4635	*Mammuthus primigenius*	3452	2813	3381
Mammuthus primigenius	4265	4779	5820	*Mammuthus meridionalis*	6254	6117	5865
Mammuthus primigenius	4610	6235	6023	*Mammut americanum*	3359	3397	3558
Mammuthus primigenius	3278	4381	4491	*Mammut americanum*	4663	7672	8129
Mammuthus primigenius	4302	5688	5491	*Mammut americanum*	3267	6117	5302
Mammuthus columbi	6630	6424	6646	*Mammut americanum*	4599	6385	7385
Mammut americanum	5639	7005	6645	*Mammut americanum*	3743	4991	7024
Mammut americanum	6772	7072	6639	*Mammut americanum*	4276	4204	6375
Mammut americanum	5639	5453	5455	*Gomphotherium productum*	1945	4991	4456
Gomphotherium productum	4265	4252	4244	*Gomphotherium productum*	1354	2405	2694
Gomphotherium productum	3897	3638	3920	*Gomphotherium productum*	1772	3993	3971
Gomphotherium productum	3897	3226	3222	*Gomphotherium productum*	1261	2405	2753
Serbelodon barbourensis	4416	5928	5370	*Gomphotherium productum*	2833	3688	4806
Serbelodon barbourensis	3755	3360	3357	*Gomphotherium productum*	2010	4045	5010
Palaeomastodon beadnelli	–	4025	3691	*Cuvieronius hyodon*	2824	6799	6547
Palaeomastodon beadnelli	1022	1341	671	*Amebelodon floridanus*	2824	3688	3359
Amebelodon floridanus	2742	4644	4632	**Tibia**			
Deinotherium giganteum	12221	15753	14580	*Mammuthus primigenius*	3362	2787	3493
Radius				*Mammuthus primigenius*	3640	2250	3940
Elephas antiquus	4665	5858	5371	*Mammuthus primigenius*	4281	2811	4405
Mammuthus imperator	5045	3466	3767	*Mammuthus columbi*	7859	4980	6274
Gomphotherium productum	1993	2178	2269	*Gomphotherium productum*	5712	3770	5000
Ulna				*Gomphotherium productum*	7599	3931	6568
Elephas antiquus	5992	4192	5530	*Gomphotherium productum*	5292	3297	5131
Elephas antiquus	8808	–	8724	*Deinotherium giganteum*	17720	10689	9774
Mammuthus primigenius	3059	2873	3020				
Mammut americanum	6644	3863	6592				
Serbelodon barbourensis	3009	987	2993				
Palaeomastodon beadnelli	1080	555	973				

of around 1500 mm, implying a body mass of around 11 900 kg. Both specimens appear to have been subequal to the largest specimen used in this analysis (Appendix 2, Table 7). Even larger specimens appear to have been discovered, and a partial femur was restored at around 1600 mm (Osborn, 1942), implying a body mass of around 14 500 kg.

Elephas antiquus, *E. recki*, *Mammuthus meridionalis*, *M. columbi* and, in part, *M. imperator* all appear to have been considerably larger than extant elephants, and *Deinotherium giganteum* appears to have been equally as large as the giant elephantids. It is worth bearing in mind that the fossils recovered are best taken as indicative of the average sizes of the various species. Among extant elephants, record specimens can be considerably larger than average specimens (Wood, 1981; McFarlan, 1992; see also Pilla, 1941; Blashford-Snell & Lenska, 1996), indicating that particularly large bulls of the giant fossil species may have approached 20 000 kg in body mass, perhaps even exceeded this value. The largest proboscidean appears to have been either *Deinotherium giganteum* or *Mammuthus trogontherii*.

According to Garrutt & Nikolskaja (1988), the Mosbach *M. trogontherii* had a humerus of 144 cm, and Osborn (1942) was of the opinion that this animal would have had a shoulder height of around 450 cm in the flesh. A humerus of 1440 mm would imply a body mass of around 15 000 kg (Table 3), and a shoulder height of 450 cm would imply a body mass of 13 866 kg (eqn 1), 12 117 kg (eqn 2), 18 201 kg (eqn 3) and 18 822 kg (eqn 6). An exceptionally large *M. trogontherii* bull may well have exceeded 20 000 kg in body mass. Another specimen had a femur of 1430 mm (Osborn, 1942), implying a body mass of around 10 300 kg.

Proboscideans weighing 10 000–15 000 kg would have required a substantial amount of fodder every day, and could potentially have been very important at forming the landscape, as with extant elephants (Buss, 1961; Laws *et al*., 1975; Moss, 1988; Haynes, 1991). The basal metabolic rate (BMR) decreases with increasing body size to about the $\text{Mass}^{0.75}$ (Kleiber, 1961; McNab, 1974, 1983; Mellett, 1982; Nagy, 1987; Eckert, Randall & Augustine, 1988; Schmidt-Nielsen, 1995). However, this value does not reflect the actual energy needs of the animals, as it only deals with resting metabolism. The field metabolic rate (FMR) is more relevant because it addresses the total energy budget of the animal, and it also shows a mass-specific decrease with increasing body size, but it is not a simple multiplication of the BMR (Nagy, 1987). The mass-specific basal and field metabolic rates are lower for herbivores subsisting on low-calorie, fibre-rich foods than for carnivores, and in very large species in general (McNab, 1974, 1983, 1986; Calder & Dawson, 1978; Nagy, 1987).

An Asian elephant of 3833 kg consumed 268 litres of oxygen h^{-1} (Eckert *et al*., 1988), or 6342 litres day^{-1}, providing that the basal metabolism was constant throughout the day, which is unlikely, as it should be lower during sleep. Assuming a respiratory quotient of around 0.8, as in most animals (Eckert *et al*., 1988; see also Zubay, 1989), this implies a BMR of 30 874 kcal day^{-1}, 90% of the predicted BMR of 34 100 kcal day^{-1} ($70 \times \text{Mass}^{0.75}$; see McNab, 1974), in accordance with the above. The actual caloric intake will depend on the composition of the food and assimilation rates, which in elephants are rather low because of the poor degree of mastication and short intestines, resulting in very nutritious dung filled with discernible food remains (Benedict, 1936; Laws *et al*., 1975). The digestive efficiency of the Asian elephant has been found to be around 40% (Benedict, 1936), considerably below the assimilation rates of cattle, horses and sheep (Benedict, 1936), deer (Drodz & Osiecki, 1973), rodents and lizards (Drodz, 1975; Karasov & Diamond, 1985) and cats (Golley *et al*., 1965).

Assessed feeding rates of wild elephants often leads to very high estimates in comparison with both their predicted energy needs and their food consumption in captivity. Feeding rates of wild bull African elephants are often assessed to be as high as 300 kg, and around 150 kg for cows (Laws & Parker, 1968; Laws, 1970a, b; Guy, 1975 (citing 170 kg day^{-1} for bulls); Laws *et al*., 1975). In Asian elephant bulls, feeding rates of 150 kg day^{-1} have been assessed (Vancuylenberg, 1977). Observations on captive elephants support the notion of exaggerated feeding rates being ascribed to wild elephants, probably because the daily feeding cycle of 12–14 h day^{-1} (Guy, 1975, see also table 2, p. 4) or even 17–19 h day^{-1} (Vancuylenberg, 1977) involves long periods of low-intensity feeding (see also Guy, 1976). If indeed the exaggerated values were true, one would have to wonder how, if at all, fossil proboscideans could sustain body sizes sometimes far exceeding those of extant elephant, unless they fed on substantially more nutritious items. For this reason alone, the above values appear suspect.

Assuming fossil proboscideans had similar size-specific metabolic rates and assimilation rates as modern elephants, a 10 000 kg *Mammuthus* or *Elephas* would have had an estimated FMR of 175 000 kcal day^{-1}. A particularly large, 20 000 kg *Mammuthus* or *Deinotherium* would have a predicted FMR of 289 000 kcal day^{-1}. These requirements would have been increased during migration, and evidently such amounts of food intake would imply moving around in a continuous fashion so as not to deplete any one area, perhaps to a greater extent than in extant elephants (see Buss, 1961; Laws *et al*., 1975). Possibly this could have affected population size, and hence extinction rates, causing really giant proboscideans to be a rare phenomenon (see Farlow, 1993), which indeed they seem to have been.

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APPENDIX 1

Bone measurements and estimated body masses of fossil proboscideans, skeletons or partial skeletons. All measurements are in millimetres and body masses are in kilograms. The values in bold type are the mass values computed by the relevant equations from Tables 2 and 3. Numbers in italic (humerus diaphysis lateromedial diameter and femur medial condyle length) were computed with restricted data sets, as noted in Tables 3 and 4.

Mammuthus primigenius The Hebior Mammoth, shoulder height of mounted skeleton 318 cm

	Humerus		Radius		Ulna		Femur		Tibia		Fibula	
Length	1037	**6341.55**	775	**5536.92**	860	**5137.66**	1203	**6068.46**	682	**4728.89**	623	**4794.61**
Circ.	350	**4432.75**	173	**5292.50**	291	**4296.91**	377	**5439.84**	301	**6852.07**	93	**4412.84**
Diap.ap	109	**3897.26**	68	**6183.05**	88	**4047.06**	80	**3119.78**	88	**5714.10**	29.5	**3561.93**
Diap.lm	113.5	**5074.91**	42	**4037.50**	97	**4455.17**	160	**7164.15**	104	**5701.65**	30	**6523.04**
Diap.lm			*42*	***3517.53***								
Art.w	299	**19788.14**					229	**8250.87**				
Med.con.l	168	**9901.51**					183	**24667.90**				
Med.con.l							*183*	***11432.46***				
Med.con.w	115	**6649.88**					112	**6465.73**				
Lat.con.l	123	**5000.37**					139	**21917.20**				
Lat.con.w	91	**4092.39**					96	**6740.87**				
Avge		**7286.31**	Avge[2]	**5262.49**	Avge	**4484.20**	Avge[4]	**9992.64**	Avge	**5749.18**	Avge	**4823.10**
Avge[1]		**5723.83**	Avge[3]	**5132.50**			Avge[5]	**8502.07**				
							Avge[6]	**6847.64**				

[1]Excluding Art.w; [2]Diap.lm; [3]*Diap.lm*; [4]Med.con.l; [5]Med.con.l, excl. Lat.con.l; [6]*Med.con.l*, excl. Lat.con.l

Mammuthus primigenius, Brussels, shoulder height of mounted skeleton 325 cm

	Humerus		Radius		Ulna		Femur		Tibia		Fibula	
Length	1198	**9276.25**	839	**6818.53**	976	**7205.80**	1273	**7205.24**	767	**6252.64**	732	**7084.57**
Circ.	423	**6550.59**	149	**3925.59**	353	**6350.01**	419	**6771.71**	331	**8811.07**	78	**3051.79**
Diap.ap	137	**6169.50**	49	**3389.69**	115.5	**7571.68**	108.5	**6317.29**	104	**7213.79**	30.5	**3715.10**
Diap.lm	132	**6994.05**	46	**4850.60**	109	**5459.82**	158	**6994.60**	107	**5931.77**	19	**3744.67**
Diap.lm			*46*	***4207.38***								
Art.w	334	**30378.91**					287	**18189.44**				
Med.con.l	201	**16785.46**					194	**31519.51**				
Med.con.l							*194*	***12965.38***				
Med.con.w	140	**13003.51**					103	**5271.38**				
Lat.con.l	201	**20445.43**					135	**19305.77**				
Lat.con.w	134	**17637.35**					108	**9259.49**				
Avge		**14137.89**	Avge[3]	**4746.10**	Avge	**6646.83**	Avge[5]	**12314.94**	Avge	**7052.32**	Avge	**4399.03**
Avge[1]		**12107.77**	Avge[4]	**4585.30**			Avge[6]	**9121.82**				
Avge[2]		**10916.67**					Avge[7]	**7626.44**				

[1]Excl. Art.w; [2]Excl. Art.w and Lat.con.l; [3]Diap.lm; [4]*Diap.lm*; [5]Med.con.l; [6]*Med.con.l*, excl. Lat.con.l; [7]*Med.con.l*, excl. Art.w & Lat.con.l

Mammuthus primigenius, Paris

	Humerus		Radius		Ulna		Femur		Tibia		Fibula	
Length	878	**4089.81**	707	**4351.30**	667	**2604.21**	1071	**4264.20**	572	**3112.49**	554	**3608.35**
Circ.	319	**3661.34**	138	**3367.23**	316	**5076.17**	339	**4364.32**	263	**4793.99**	94	**4512.92**
Diap.ap	101	**3343.87**	56	**4330.46**	90	**4262.09**	88	**3890.10**	82	**5178.00**	34	**4261.45**
Diap.lm	102	**4044.59**	32	**2333.05**	111	**5635.67**	128	**4684.23**	85.5	**4341.48**	26	**5481.94**

APPENDIX 1 *Continued*

	Humerus		Radius		Ulna		Femur		Tibia		Fibula	
Diap.lm			*32*	***2059.47***								
Avge		**3784.90**	Avge[1]	**3595.51**	Avge	**4394.53**	Avge	**4300.71**	Avge	**4356.49**	Avge	**4466.17**
			Avge[2]	**3527.11**								

[1]Diap.lm; [2]*Diap.lm*

Mammuthus primigenius, FMNH

	Humerus		Femur		Tibia	
Length	906	**4442.55**	1111	**4766.32**	676	**4630.56**
Circ.	392	**5599.35**	337	**4311.10**	313	**7599.01**
Diap.ap	124	**5049.62**	88.5	**3941.47**	96.5	**6498.51**
Diap.lm	126	**6335.97**	126	**4545.86**	103	**5625.51**
Art.w	228	**6925.99**	195	**4699.86**		
Med.con.l	186	**13359.77**	146	**9554.71**		
Med.con.l			*146*	***7025.53***		
Med.con.w	111	**5893.84**	112	**6564.73**		
Lat.con.l	142	**7548.85**	116	**9987.65**		
Lat.con.w	73	**1780.86**	89	**5496.56**		
Avge		**6326.31**	Avge[2]	**5985.36**	Avge	**6088.40**
Avge[1]		**5970.88**	Avge[3]	**5168.93**		

[1]Excl. Med.con.l. & Lat.con.l; [2]Med.con.l; [3]*Med.con.l*, excl. Lat.con.l

Mammuthus primigenius, FMNH PM26267

	Ulna		Femur	
Length	737	**3400.58**	1014	**3611.86**
Circ.	321	**5239.90**	391	**5867.04**
Diap.ap	99.5	**5370.49**	98	**4990.98**
Diap.lm	105	**5115.28**	151	**6416.38**
Art.w			227	**8001.29**
Med.con.l			155	**12282.95**
Med.con.l			*155*	***7992.43***
Med.con.w			106	**5683.08**
Lat.con.l			122	**12434.40**
Lat.con.w			105	**8582.46**
Avge		**4781.56**	Avge[1]	**7541.16**
			Avge[2]	**6393.19**

[1]Med.con.l; [2]*Med.con.l*, excl. Lat.con.l

Mammuthus meridionalis, Paris, shoulder height of mounted skeleton 383 cm.

	Humerus		Radius		Ulna		Femur		Tibia		Fibula	
Length	1255	**10485.08**	869	**7476.98**	1084	**9539.87**	1451	**10720.28**	856	**8117.88**	834	**9716.36**
Circ.	485	**8684.37**	190	**6384.08**	405	**8384.06**	446	**7707.81**	352	**10368.94**	113	**6638.80**
Diap.ap	143	**6724.34**	67	**6017.29**	123	**8752.53**	118	**7672.35**	107	**7505.74**	45	**6071.66**
Diap.lm	166	**11380.44**	54	**6702.55**	135	**7927.87**	166	**7684.36**	117.5	**6756.95**	27	**5739.18**
Diap.lm			*54*	***5768.90***								
Avge		**9318.56**	Avge[1]	**6645.22**	Avge	**8651.08**	Avge	**8446.20**	Avge	**8187.38**	Avge	**7041.50**
			Avge[2]	**6411.81**								

[1]Diap.lm; [2]*Diap.lm*

APPENDIX 1 *Continued*

Mammuthus meridionalis, Paris, mounted forelimb

	Humerus		Radius		Ulna	
Length	1287	**11204.39**	1042	**12039.80**	1161	**11461.00**
Circ.	459	**7751.89**	206	**7504.90**	384	**7528.27**
Diap.ap	156	**8008.84**	69	**6350.86**	107	**6349.17**
Diap.lm	136	**7451.93**	62	**8856.19**	138	**8237.55**
Diap.lm	*62*	***7571.84***				
Avge		**8604.27**	Avge[2]	**8687.94**	Avge	**8394.00**
Avge[1]		**7737.56**	Avge[3]	**7142.53**	Avge[4]	**7371.67**

[1]Excl. Length; [2]Diap.lm; [3]*Diap.lm*, excl. Length; [4]Excl. Length

Mammuthus imperator, DMNH 1359

	Humerus		Femur		Tibia	
Length	1240	**10158.04**	1370	**9004.72**	840	**7761.69**
Circ.	502	**9323.59**	483	**9092.77**	385	**13144.34**
Diap.ap	162	**8639.71**	127	**9095.71**	120	**8807.77**
Diap.lm	167.5	**10178.15**	181	**9060.37**	125	**7364.46**
Avge		**9574.87**	Avge	**9063.39**	Avge	**9269.56**
					Avge[1]	**7977.97**

[1]Excl. Circ.

Mammuthus imperator, AMNH 10598

	Humerus		Radius		Ulna	
Length	1205	**9419.77**	958	**9656.94**	1082	**9492.88**
Circ.	491	**8907.31**	215	**8175.18**	415	**8807.94**
Diap.ap	152.5	**7651.93**	69.5	**6435.53**	118.5	**8032.41**
Diap.lm	160.5	**10594.38**	77	**13709.78**	145.5	**9033.77**
Diap.lm			*77*	***11599.49***		
Avge		**9143.35**	Avge[1]	**9494.36**	Avge	**8841.75**
			Avge[2]	**8966.78**		

[1]Diap.lm; [2]*Diap.lm*

Mammuthus imperator, AMNH 26820A

	Humerus		Ulna		Femur		Tibia	
Length	1177	**8853.85**	869	**5282.67**	1236	**6588.08**	729	**5540.97**
Circ.	417	**6360.48**	328	**5473.53**	386	**5712.55**	305	**7095.72**
Diap.ap	126	**5214.58**	100	**5432.87**	98	**4990.98**	89.5	**5850.44**
Diap.lm	139.5	**7865.21**	109	**5459.82**	148	**6175.83**	104.5	**5739.82**
Avge		**7073.53**	Avge	**5412.22**	Avge	**5866.86**	Avge	**6056.74**

Mammuthus imperator, AMNH 26821A

	Humerus		Femur	
Length	1192	**9154.32**	1399	**9595.95**
Circ.	436	**6972.39**	410	**6473.60**

APPENDIX 1 *Continued*

	Humerus		Femur	
Diap.ap	132	**5725.45**	112.5	**6869.63**
Diap.lm	145.5	**8601.20**	148.5	**6215.62**
Avge		**7613.34**	Avge	**7288.70**

Mammut americanum, FMNH P3945

	Humerus		Ulna		Femur		Tibia	
Length	924	**4678.95**	803	**4277.00**	1124	**4937.66**	731	**5577.19**
Circ.	443	**7205.13**	371	**7021.83**	430	**7145.51**	328	**8601.28**
Diap.ap	145	**6914.62**	123	**8752.53**	81.5	**3256.89**	89	**5804.89**
Diap.lm	137	**7568.81**	113	**5813.89**	184	**9348.45**	120	**6957.81**
Art.w					254	**11859.48**		
Med.con.l					168	**17225.57**		
Med.con.l					*168*	***9507.73***		
Med.con.w					123	**8390.51**		
Lat.con.l					125	**13818.61**		
Lat.con.w					119	**12026.01**		
Avge		**6591.88**	Avge	**6466.31**	Avge[1]	**9778.75**	Avge	**6735.30**
					Avge[2]	**8309.03**		

[1]Med.con.l; [2]*Med.con.l*, excl. Lat.con.l

Mammut americanum, AMNH 9965

	Humerus		Tibia	
Length	871	**4004.44**	618	**3741.03**
Circ.	445	**7272.35**	333	**8952.68**
Diap.ap	147.5	**7156.22**	99	**6734.58**
Diap.lm	135.5	**7393.86**	113	**6399.61**
Avge		**6456.72**	Avge	**6456.97**

Mammut americanum, FMNH PM1173

	Radius		Ulna		Tibia	
Length	740	**4904.63**	833	**4717.67**	719	**5361.93**
Circ.	163	**4698.18**	375	**7175.76**	333	**8952.68**
Diap.ap	59	**4765.47**	116.5	**7723.55**	109	**7702.18**
Diap.lm	45	**4640.28**	122.5	**6692.48**	103	**5625.51**
Diap.lm	*45*	***4029.23***				
Avge[1]		**4752.14**	Avge	**6577.37**	Avge	**6910.58**
Avge[2]		**4599.38**				

[1]Diap.lm; [2]*Diap.lm*

Mammut americanum, AMNH 14292

	Femur		Tibia	
Length	858	**2175.07**	572	**3112.49**
Circ.	333	**4205.68**	274	**5343.12**

APPENDIX 1 *Continued*

	Femur		Tibia	
Diap.ap	75	**2686.76**	75.5	**4614.49**
Diap.lm	137	**5331.26**	98.5	**5286.49**
Avge		**3599.69**	Avge	**4589.14**

Archaeobelodon filholi, Paris

	Humerus		Ulna	
Length	673	**2029.45**	608	**2033.01**
Circ.	313	**3520.79**	223	**2508.57**
Diap.ap	95	**2956.73**	60	**1674.87**
Diap.lm	104	**4214.91**	80	**3183.98**
Art.w	194	**3705.93**		
Med.con.l	89	**1526.27**		
Med.con.w	66	**1001.56**		
Lat.con.l	122	**4884.68**		
Lat.con.w	84	**3025.15**		
Avge		**2985.05**	Avge	**2350.11**
Avge[1]		**3476.81**		

[1]Excl. Med.con.l & Med.con.w

Gomphotherium angustidens, Paris

	Humerus		Radius		Ulna		Femur		Tibia	
Length	678	**2069.42**	588	**2682.83**	649	**2420.53**	894	**2464.14**	576	**3164.50**
Circ.	355	**4564.28**	131	**3034.20**	255	**3289.91**	312	**3674.35**	248	**4103.89**
Diap.ap	110	**3969.43**	40	**2336.10**	76	**2887.17**	70.5	**2328.16**	65.5	**3784.76**
Diap.lm	116	**5315.30**	43.5	**4333.60**	86	**3611.85**	128.5	**4719.14**	92.5	**4843.84**
Diap.lm			*43.5*	***3769.11***						
Avge		**3979.61**	Avge[1]	**3096.68**	Avge	**3052.36**	Avge	**3296.45**	Avge	**3974.25**
			Avge[2]	**2955.56**						

[1]Diap.lm; [2]*Diap.lm*

Gomphotherium productum, AMNH 21M6

	Ulna		Tibia	
Length	492	**1154.34**	405	**1369.46**
Circ.	242	**2959.59**	185	**1889.40**
Diap.ap	70.5	**2428.39**	65.5	**3784.76**
Diap.lm	84	**3466.67**	52	**2173.44**
Avge		**2502.25**	Avge	**2304.26**
Avge[1]		**2951.55**	Avge[2]	**2615.87**

[1]Excl. Length; [2]Excl. Length

APPENDIX 1 *Continued*

Gomphotherium productum, AMNH 99039

	Ulna		Tibia	
Length	662	**2552.35**	548	**2810.87**
Circ.	304	**4693.94**	262	**4745.89**
Diap.ap	93	**4596.49**	72	**4318.82**
Diap.lm	100.5	**4739.19**	94.5	**4990.18**
Avge		**4145.49**	Avge	**4216.44**
Avge[1]		**4676.54**	Avge[2]	**4684.96**

[1] Excl. Length; [2] Excl. Length

Cuvieronius hyodon, Paris

	Humerus		Radius		Ulna		Femur		Tibia		Fibula	
Length	685	**2126.20**	509	**1837.29**	592	**1893.10**	944	**2906.82**	612	**3655.23**	573	**3915.36**
Circ.	347	**4354.78**	130	**2988.04**	268	**3637.89**	391	**5867.04**	338	**9312.88**	133	**9342.86**
Diap.ap	97	**3083.13**	29	**1295.13**	79	**3156.49**	103	**5600.44**	117	**8502.10**	42	**5564.98**
Diap.lm	124	**6124.24**	54	**6702.55**	81.5	**3288.79**	147	**6096.62**	98	**5249.19**	43	**10102.47**
Diap.lm			*54*	***5768.90***								
Art.w	221	**6138.18**					235	**9032.98**				
Med.con.l	128	**4447.52**					155	**12282.95**				
Med.con.l							*155*	***7992.43***				
Med.con.w	93	**3224.31**					96	**4383.92**				
Lat.con.l	129	**5732.10**					127	**14805.29**				
Lat.con.w	95	**4813.98**					106	**8804.55**				
Avge		**4449.38**	Avge[2]	**3205.75**	Avge	**2994.07**	Avge[5]	**7753.40**	Avge	**6679.85**	Avge	**7231.42**
Avge[1]		**4739.78**	Avge[3]	**2972.34**	Avge[4]	**3361.06**	Avge[6]	**6335.60**			Avge[7]	**6274.40**

[1] Excl. Length; [2] Diap.lm; [3] *Diap.lm*; [4] Excl. Length; [5] Med.con.l; [6] *Med.con.l*, excl. Lat.con.l.; [7] Excl. Diap.lm

Eubelodon morrilli, AMNH 25708A

	Humerus		Ulna	
Length	906	**4442.55**	665	**2583.39**
Circ.	421	**6486.90**	327	**5439.84**
Diap.ap	129.5	**5509.68**	103.5	**5880.92**
Diap.lm	138.5	**7745.92**	104.5	**5072.89**
Avge		**6046.26**	Avge	**4744.26**
			Avge[1]	**5464.55**

[1] Excl. Length

Stegomastodon platensis, AMNH 11198

	Humerus		Femur	
Length	893	**4276.53**	963	**3088.10**
Circ.	466	**7997.58**	352	**4718.47**
Diap.ap	135.5	**6034.53**	98	**4990.98**
Diap.lm	161.5	**10735.09**	126	**4545.86**
Avge		**7260.93**	Avge	**4335.85**
Avge[1]		**6102.88**		

[1] Excl. Diap.lm

APPENDIX 2

Bone measurements and estimated body masses of fossil proboscideans, individual bones only. All measurements are in millimetres and body masses are in kilograms. The values in bold type are the mass values computed by the relevant equations from Tables 2 and 3. Numbers in italic (humerus diaphysis lateromedial diameter and femur medial condyle length) were computed with restricted data sets, as noted in Tables 3 and 4

Humerus

	Elephas antiquus		*Elephas antiquus*		*Elephas antiquus*	
Length	1000	**5762.53**	1332	**12266.55**	1005	**5838.77**
Circ.	382	**5308.87**	565	**11896.86**	398	**5777.47**
Diap.ap	122.5	**4927.65**	161.5	**8586.22**	129.5	**5509.68**
Diap.lm	121	**5813.78**	168	**11673.67**	123.5	**6071.90**
Avge		**5453.21**	Avge	**11105.83**	Avge	**5799.46**

	Elephas antiquus		*Elephas antiquus*	
Length	1009	**5900.22**	–	
Circ.	389	**5511.37**	575	**12335.02**
Diap.ap	121	**4807.17**	168	**9294.61**
Diap.lm	126.5	**6389.49**	197.5	**16460.73**
Art.w	298	**19533.09**	357	**39315.97**
Med.con.l	186	**13359.77**	242	**28928.27**
Med.con.w	101	**4271.85**	141	**13322.90**
Lat.con.l	159	**10439.90**	177	**14198.73**
Lat.con.w	74	**1874.72**	107	**7542.70**
Avge		**8009.73**	Avge	**17674.87**
Avge[1]		**5376.02**	Avge[2]	**13122.40**

[1]Excl. Art.w, Med.con.l, Lat.con.l & w; [2]Excl. Art.w, Med.con.l & Lat.con.w

	Mammuthus primigenius		*Mammuthus primigenius*		*Mammuthus primigenius*	
Length	1225	**9837.41**	874	**4040.89**	862	**3896.32**
Circ.	523	**10145.52**	314	**3544.01**	316	**3590.71**
Diap.ap	169	**9406.10**	86	**2420.85**	106	**3684.76**
Diap.lm	163.5	**11019.45**	114	**5122.51**	95	**3477.65**
Avge		**10102.12**	Avge	**3782.07**	Avge	**3662.36**

	Mammuthus primigenius		*Mammuthus primigenius*		*Mammuthus primigenius*	
Length	798	**3179.50**	828	**3504.26**	–	
Circ.	307	**3383.07**	369	**4943.13**	363	**4778.86**
Diap.ap	93	**2833.00**	108	**3825.77**	114	**4264.75**
Diap.lm	102	**4044.59**	126.5	**6389.49**	116.5	**5364.08**
Art.w			189	**3349.54**	225	**6579.71**
Med.con.l			149	**6954.98**	201	**16785.46**
Med.con.w			93	**3224.31**	112	**6076.83**
Lat.con.l	116	**4227.02**	122	**4884.68**	144	**7857.75**
Lat.con.w	65	**1149.02**	67	**1288.29**	80	**2516.26**
Avge		**3136.03**	Avge	**4262.72**	Avge	**6777.96**
Avge[1]		**3533.44**	Avge[2]	**4634.52**	Avge[3]	**5820.33**

[1]Excl. Lat.con.w; [2]Excl. Lat.con.w; [3]Excl. Med.con.l & Lat.con.w

APPENDIX 2 *Continued*

	Mammuthus primigenius		*Mammuthus primigenius*	
Length	–		831	**3537.82**
Circ.	413	**6235.34**	348	**4380.69**
Diap.ap	118.5	**4609.71**	100	**3277.69**
Diap.lm	144	**8413.94**	121	**5813.78**
Art.w	262	**11864.39**	204	**4502.22**
Med.con.l	182	**12531.73**	153	**7518.95**
Med.con.w	113	**6263.80**	97	**3722.09**
Lat.con.l	131	**5990.63**	105	**3176.62**
Lat.con.w	94	**4625.46**	61	**904.06**
Avge		**7566.87**	Avge	**4092.66**
Avge[1]		**6023.15**	Avge[2]	**4491.23**

[1]Excl. Art.w & Med.con.l; [2]Excl. Lat.con.w

	Mammuthus primigenius		*Mammuthus columbi*	
Length	903	**4403.89**	1094	**7301.91**
Circ.	395	**5688.05**	419	**6423.53**
Diap.ap	114.5	**4302.41**	142	**6630.20**
Diap.lm	137	**7568.81**	125	**6229.63**
Avge		**5490.79**	Avge	**6646.32**

	Mammut americanum		*Mammut americanum*		*Mammut americanum*	
Length	958	**5146.42**	966	**5260.45**	975	**5390.60**
Circ.	437	**7005.40**	439	**7071.65**	387	**5453.11**
Diap.ap	131	**5638.64**	143.5	**6771.66**	126	**5214.58**
Diap.lm	147	**8790.65**	136	**7451.93**	120.5	**5762.86**
Avge		**6645.28**	Avge	**6638.93**	Avge	**5455.29**

	Gomphotherium productum		*Gomphotherium productum*		*Gomphotherium productum*	
Length	646	**1821.85**	653	**1874.35**	570	**1309.98**
Circ.	343	**4251.92**	318	**3637.71**	300	**3225.96**
Diap.ap	114	**4264.75**	109	**3897.27**	109	**3897.26**
Diap.lm	104	**4214.91**	93	**3323.97**	82	**2544.07**
Avge		**3638.36**	Avge	**3183.32**	Avge	**2744.32**
Avge[1]		**4243.86**	Avge[2]	**3919.65**	Avge[3]	**3222.43**

[1]Excl. Length; [2]Excl. Length; [3]Excl. Length

	Serbelodon barbourensis		*Serbelodon barbourensis*	
Length	801	**3211.10**	576	**1346.63**
Circ.	403	**5928.10**	306	**3360.39**
Diap.ap	116	**4416.40**	107	**3754.93**
Diap.lm	140	**7925.21**	88	**2955.81**
Avge		**5370.30**	Avge	**2854.44**
			Avge[1]	**3357.04**

[1]Excl. Length

APPENDIX 2 *Continued*

	Palaeomastodon beadnelli		*Palaeomastodon beadnelli*	
Length	666	**1974.29**	414	**564.01**
Circ.	334	**4025.12**	196	**1341.38**
Diap.ap	–*		56	**1022.49**
Diap.lm	–*		69	**1763.15**
Art.w	203	**4417.35**	105	**343.93**
Med.con.l	124	**4050.77**	67.5	**676.40**
Med.con.w	94	**3344.04**	50	**388.70**
Lat.con.l	117	**4332.36**	49	**357.17**
Lat.con.w	50	**426.76**	40	**183.80**
Avge		**3224.38**	Avge	**737.89**
Avge[1]		**3690.66**	Avge[2]	**670.58**

*Diaphysis distorted.
[1]Excl. Lat.con.w; [2]Excl. Diap.lm & Lat.con.w

Radius

	Elephas antiquus		*Mammuthus imperator*		*Gomphotherium productum*	
Length	726	**4664.88**	748	**5044.98**	525	**1992.72**
Circ.	182	**5857.65**	140	**3465.56**	111	**2178.25**
Diap.ap	45	**2899.49**	50	**3517.66**	27	**1136.02**
Diap.lm	64	**9441.82**	39	**3476.97**	43.5	**4333.60**
Diap.lm	*64*	***8060.17***	*39*	***3040.05***	*43.5*	***3769.11***
Avge[1]		**5715.96**	Avge[3]	**3876.29**	Avge[5]	**2410.15**
Avge[2]		**5370.54**	Avge[4]	**3767.06**	Avge[6]	**2269.03**

[1]Diap.lm; [2]*Diap.lm*; [3]Diap.lm; [4]*Diap.lm*; [5]Diap.lm; [6]*Diap.lm*

Ulna

	Elephas antiquus		*Elephas antiquus*		*Mammuthus primigenius*	
Length	797	**4192.09**	–		692	**2873.43**
Circ.	343	**5991.52**	415	**8807.94**	246	**3059.34**
Diap.ap	106	**6213.32**	124	**8917.32**	78	**3065.20**
Diap.lm	112	**5724.48**	140	**8446.81**	78.5	**3080.63**
Avge		**5530.35**	Avge	**8724.02**	Avge	**3019.65**

	Mammut americanum		*Serbelodon barbourensis*		*Palaeomastodon beadnelli*	
Length	773	**3863.03**	464	**986.96**	374	**554.54**
Circ.	361	**6644.38**	244	**3009.26**	147	**1080.06**
Diap.ap	108	**6486.70**	71	**2468.25**	40.5	**677.28**
Diap.lm	122	**6644.93**	84.5	**3502.73**	53.5	**1578.81**
Avge		**5909.76**	Avge	**2491.80**	Avge	**972.67**
Avge[1]		**6592.00**	Avge[2]	**2993.41**		

[1]Excl. Length; [2]Excl. Length

APPENDIX 2 *Continued*

Femur

	Elephas recki		*Elephas recki*		*Elephas recki*	
Length	1030	**3787.67**	1165	**5505.02**	1360	**8806.65**
Circ.	324	**3973.42**	413	**6572.20**	505	**9972.51**
Diap.ap	83.5	**3444.93**	106	**5986.37**	130	**9600.92**
Diap.lm	122	**4275.02**	157	**6910.55**	192	**10137.57**
Avge		**3870.26**	Avge	**6243.28**	Avge	**9629.41**

	Elephas recki		*Elephas antiquus*		*Elephas antiquus*	
Length	1505	**11977.97**	1075	**4312.74**	1169	**5562.60**
Circ.	505	**9972.51**	373	**5320.85**	348	**4607.98**
Diap.ap	124	**10298.78**	102	**5475.35**	93.5	**4476.31**
Diap.lm	188	**9739.22**	136	**5111.17**	128	**4684.23**
Art.w					224	**7637.10**
Med.con.l					202	**37348.26**
Med.con.l					*202*	***14145.41***
Med.con.w					110	**6262.10**
Lat.con.l					141	**23320.73**
Lat.con.w					101	**7729.43**
Avge		**10497.12**	Avge	**5055.03**	Avge[1]	**11292.08**
					Avge[2]	**6888.14**

[1]Med.con.l; [2]*Med.con.l*, excl. Lat.con.l

	Mammuthus primigenius		*Mammuthus primigenius*		*Mammuthus primigenius*	
Length	1280	**7326.20**	1023	**3710.06**	1032	**3810.05**
Circ.	499	**9728.41**	368	**5174.03**	328	**4075.80**
Diap.ap	137.5	**10932.32**	86.5	**3738.29**	88.5	**3941.47**
Diap.lm	180	**8965.29**	147.5	**6136.16**	120.5	**4175.49**
Art.w			185	**3908.67**	179	**3482.49**
Med.con.l			130	**5868.78**	124	**4812.58**
Med.con.l			*130*	***5470.37***	*124*	***4940.60***
Med.con.w			97	**4504.55**	90	**3702.09**
Lat.con.l			105	**6478.37**	107	**7031.85**
Lat.con.w			83	**4553.98**	81	**4264.22**
Avge		**9238.05**	Avge[1]	**4896.99**	Avge[3]	**4366.26**
			Avge[2]	**4852.72**	Avge[4]	**4380.48**

[1]Med.con.l; [2]*Med.con.l*; [3]Med.con.l; [4]*Med.con.l*

	Mammuthus primigenius		*Mammuthus meridionalis*	
Length	999	**3452.20**	1215	**6254.10**
Circ.	247	**2263.70**	385	**5681.91**
Diap.ap	76.5	**2812.82**	107	**6116.91**
Diap.lm	113	**3694.59**	138	**5405.60**
Art.w	163	**2508.97**		
Med.con.l	129	**5681.54**		
Med.con.l	*129*	***5380.06***		
Med.con.w	82	**2901.03**		
Lat.con.l	95	**4193.83**		
Lat.con.w	73	**3221.92**		
Avge[1]		**3414.50**	Avge	**5864.63**
Avge[2]		**3381.00**		

[1]Med.con.l; [2]*Med.con.l*

APPENDIX 2 *Continued*

	Mammut americanum		*Mammut americanum*		*Mammut americanum*	
Length	990	**3358.53**	1103	**4662.89**	981	**3266.69**
Circ.	317	**3797.49**	460	**8217.93**	368	**5174.03**
Diap.ap	83	**3397.36**	118	**7672.35**	107	**6116.91**
Diap.lm	119	**4077.08**	175	**8497.06**	127	**4614.80**
Avge		**3557.61**	Avge	**7262.56**	Avge	**4793.11**
			Avge[1]	**8129.11**	Avge[2]	**5301.91**

[1]Excl. Length; [2]Excl. Length.

	Mammut americanum		*Mammut americanum*		*Mammut americanum*	
Length	1098	**4599.01**	1026	**3743.19**	1072	**4276.30**
Circ.	460	**8217.92**	433	**7249.27**	381	**5560.19**
Diap.ap	109	**6384.89**	98	**4990.98**	91	**4204.06**
Diap.lm	194	**10339.59**	178	**8776.57**	151.5	**6456.90**
Art.w			227	**8001.29**	223	**7518.38**
Med.con.l			179	**22481.74**	150	**10703.04**
Med.con.l			*179*	***10900.59***	*150*	***7447.02***
Med.con.w			104	**5406.49**	103	**5271.38**
Lat.con.l			129	**15845.33**	113	**8912.93**
Lat.con.w			98	**7126.10**	101	**7729.43**
Avge		**7385.35**	Avge[2]	**9291.22**	Avge[4]	**6736.96**
Avge[1]		**8314.13**	Avge[3]	**7024.31**	Avge[5]	**6375.18**

[1]Excl. Length; [2]Med.con.l; [3]Med.con.l, excl. Lat.con.l; [4]Med.con.l; [5]Med.con.l

	Gomphotherium productum		*Gomphotherium productum*		*Gomphotherium productum*	
Length	827	**1945.16**	734	**1354.15**	802	**1772.08**
Circ.	339	**4364.32**	270	**2722.64**	324	**3973.42**
Diap.ap	98	**4990.98**	71.5	**2405.33**	89	**3993.22**
Diap.lm	118	**4012.09**	100.5	**2955.46**	117	**3947.60**
Avge		**3828.14**	Avge	**2359.39**	Avge	**3421.58**
Avge[1]		**4455.79**	Avge[2]	**2694.47**	Avge[3]	**3971.41**

[1]Excl Length; [2]Excl Length; [3]Excl Length

	Gomphotherium productum		*Gomphotherium productum*		*Gomphotherium productum*	
Length	717	**1261.16**	936	**2832.67**	836	**2010.14**
Circ.	273	**2785.73**	360	**4943.53**	346	**4553.24**
Diap.ap	71.5	**2405.33**	86	**3688.45**	89.5	**4045.35**
Diap.lm	102.5	**3068.45**	143	**5784.63**	130.5	**4859.97**
Art.w					194	**4616.01**
Med.con.l					146	**9554.71**
Med.con.l					*146*	***7025.53***
Med.con.w					100	**4878.65**
Lat.con.l					114	**9260.74**
Lat.con.w					86.5	**5090.25**
Avge		**2380.17**	Avge	**4312.32**	Avge[3]	**5429.90**
Avge[1]		**2753.17**	Avge[2]	**4805.54**	Avge[4]	**5009.90**

[1]Excl. Length; [2]Excl. Length; [3]Med.con.l; [4]*Med.con.l*, excl. Length & Lat.con.l

APPENDIX 2 *Continued*

	Cuvieronius hyodon		*Amebelodon floridanus*		*Amebelodon floridanus*	
Length	935	**2823.50**	935	**2823.50**	926	**2741.79**
Circ.	411	**6506.38**	305	**3505.48**	349	**4635.48**
Diap.ap	112	**6799.15**	86	**3688.45**	95	**4644.33**
Diap.lm	150	**6335.71**	108.5	**3419.49**	127	**4614.80**
Avge		**5616.18**	Avge	**3359.23**	Avge	**4159.10**
Avge[1]		**6547.08**			Avge[2]	**4631.54**

[1]Excl. Length; [2]Excl. Length

	Deinotherium giganteum	
Length	1515	**12221.22**
Circ.	585	**13527.61**
Diap.ap	161	**15753.02**
Diap.lm	211.5	**12187.75**
Avge		**14580.28**

Tibia

	Mammuthus primigenius		*Mammuthus primigenius*		*Mammuthus primigenius*	
Length	546	**2786.53**	499	**2249.59**	548	**2810.87**
Circ.	230	**3361.90**	237	**3639.54**	252	**4281.41**
Diap.ap	66.5	**3865.61**	70	**4152.37**	74	**4487.09**
Diap.lm	80	**3957.85**	81	**4026.86**	87	**4447.82**
Avge		**3492.97**	Avge	**3517.09**	Avge	**4006.80**
			Avge[1]	***3939.59***	Avge[2]	***4405.44***

[1]Excl. Length; [2]Excl. Length

	Mammuthus columbi		*Gomphotherium productum*		*Gomphotherium productum*	
Length	697	**4979.98**	620	**3769.88**	631	**3930.88**
Circ.	317	**7858.75**	281	**5712.04**	313	**7599.01**
Diap.ap	93	**6172.07**	91.5	**6033.63**	95.5	**6404.76**
Diap.lm	109	**6080.61**	87.5	**4483.43**	104	**5701.65**
Avge		**6274.35**	Avge	**4999.74**	Avge	**5909.07**
					Avge[1]	***6568.47***

[1]Excl. Length

	Gomphotherium productum		*Deinotherium giganteum*	
Length	586	**3296.71**	961	**10688.98**
Circ.	273	**5291.66**	431	**17720.30**
Diap.ap	88.5	**5759.44**	114.5	**8249.73**
Diap.lm	85.5	**4341.48**	160	**10382.75**
Avge		**4672.32**	Avge	**11760.44**
Avge[1]		**5130.86**	Avge[2]	**9773.82**

[1]Excl. Length; [2]Excl. Circ.