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IN VIVO RESTORATION AND VOLUMETRIC BODY MASS ESTIMATE OF *MAMMUTHUS MERIDIONALIS* FROM MADONNA DELLA STRADA (SCOPPITO, L'AQUILA)

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Abstract. In this contribution we present an *in vivo* reconstruction and volumetric body mass estimate for the mounted skeleton of *Mammuthus meridionalis* on exhibit at the east bastion of the Spanish Fortress at L'Aquila (Abruzzo, Central Italy). The reconstruction has been obtained starting from a 3D photogrammetric model of the skeleton acquired via a micro-drones and by digitally adding a percentage of soft tissues according to the conditions observed in wild specimens. By applying to the volume the density range proposed in literature for extant proboscideans we obtain an estimate of the body mass in the adult male specimen ranging from 11.3 t to 11.5 t, with average body mass equal to 11.43 t. In addition, we compare the volumetric BM estimate with the BM predictive values obtained by means of traditional regression equations based on long bones linear dimension and shoulder height. The results confirm that the volumetric method is always preferable if sufficiently complete mounted skeletons are available, since application of regression formulas to single bony element can lead to an underestimation or overestimation up to 130%. As a general indication, weight estimates in extinct tetrapods based on single measures and single bones should be totally avoided, especially in groups morphologically and phylogenetically distant from extant reference taxa.

Introduction

The mounted skeleton of *Mammuthus meridionalis* (Nesti, 1825), on exhibit at the east bastion of the Spanish Fortress at L'Aquila (Abruzzo, Central Italy), represents a real iconic symbol for the city of L'Aquila and the surrounding community (Rossi et al. 2017; Romano et al. 2021a). The specimen was found in a quite good state of preservation in 1954 in a sandy layer outcropping at Santarelli clay quarry in the locality Madonna della Strada (Scoppito, L'Aquila) (Maccagno 1958, 1962; Magri et al. 2010; Mancini et al. 2012; Agostini et al. 2014; Rossi et al. 2017). The skeleton was found associated with other faunal elements, including *Stephanorhinus* sp.

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Fig. 1 - The mounted skeleton of *Mammuthus meridionalis* (Nesti, 1825), on exhibit at the east bastion of the Spanish Fortress at L'Aquila (Abruzzo, Central Italy) after the new restoration project.

(*Stephanorhinus* aff. *S. hundsheimensis* Toula, 1902 according to some authors, or *Stephanorhinus etruscus* Falconer, 1868 according to others), large deer, possibly *Eucladoceros giuli* Kahlke, 1997, and *Hippopotamus antiquus* Desmarest, 1822 (see Maccagno 1962; Magri et al. 2010; Mancini et al. 2012; Rossi et al. 2017). The mammoth skeleton and associated faunal element can be chronologically constraint to an age of 1.3 Ma, obtained via palynological data from a lignitic deposit just above the fossiliferous level (Magri et al. 2010; Rossi et al. 2017).

The skeleton was returned to L'Aquila in 1960 and reassembled in the Spanish Fortress, where it was displayed until 1987, when it was disassembled and brought to Florence for a second restoration that lasted until 1991, when it was finally returned to L'Aquila and mounted in the Spanish Fortress.

From 2013 to 2015, a new restoration project has been launched and carried out thanks to the consistent financial support of "Guardia di Finanza" (contribution to the reconstruction of the city of L'Aquila) and directed by the "Direzione Regionale per i Beni Culturali e Paesaggistici dell'Abruzzo" (MIBACT), as part of the reconstruction projects following the great earthquake that struck L'Aquila in 2009. The skeleton was disassembled again, with a new restoration and detailed study conducted thanks to the latest innovative methodologies and technologies available in the paleontological and restoration fields (see Rossi et al. 2017). The skeleton was then reassembled by changing the supporting structure, in order to restore a general posture more appropriate from a biomechanical point of view (Rossi et al. 2017) (Fig. 1).

More recently, the skeleton was used as a case study to test the feasibility of using micro drones inside museum structures, as a tool to study and reconstruct in 3D large skeletons mounted on exhibit (Romano et al. 2021a). The results obtained are very encouraging, with a complete photographic survey by drone of the skeleton that took less time than traditional methods, and yielding a more defined 3D model without missing reconstructed portions (Romano et al. 2021a).

The purpose of the present contribution is three-fold: i) to propose the first *in vivo* reconstruction of the *M. meridionalis* individual from Madonna della Strada (MdS) based on the skeleton 3D model by Romano et al. (2021a) obtained with photos acquired by drone; ii) to estimate the possible body mass (BM) of the animal based on volumetric methods; and iii) to compare the obtained BM estimate with the BM predictive values obtained by means of regression equations based on long bones linear dimension and shoulder height. This to evaluate the entity of the difference between BM estimates obtained applying the regression formulas and that provided by the 3D volumetric method, which has experimentally been proved to be more precise and better performing than the estimates based on skeletal elements (see Sellers et al. 2012; Bates et al. 2015; Brassey et al. 2015; Larramendi 2016; Romano & Manucci 2019; Romano & Rubidge 2019a; Romano et al. 2021a, 2021b, 2021c).

Material and Methods

The body mass estimate and *in vivo* reconstruction of *M. meridionalis* is based on the mounted skeleton on exhibit at the east bastion of the Spanish Fortress at L'Aquila (Abruzzo, Central Italy). The specimen was registered by the Superintendence of Antiquities of Abruzzo in 1956 with n. 4246 and in 1979 by the National Museum of Abruzzo with n. OPA 1147.

In vivo restoration

The sculpture and digital reconstruction of the specimen were based on a 3D photogrammetric model of the skeleton, recently obtained by Romano et al. (2021a) using a micro drone (DJI Mavic Air 2) to take the pictures around the subject, and the software Agisoft Metashape Standard Edition, version 1.5.0 (Educational License, 64 bit) to generate a mesh model starting from 190 photos. The drone model has been preferred over the traditional camera because it was more complete, especially in the dorsal part of the specimen that was more difficult to access (see Romano et al. 2021a).

The 3D photogrammetric model has been uploaded as a "Stanford ply" file in the software for painting and sculpting ZBrush. It also allows modifying the posture of the skeleton, isolation of single bones, and correction of distortion in bony elements. Before proceeding with the reconstruction of the *in vivo* volume, the skeleton was manipulated in ZBrush to correct some anatomical details in the posture and general structure. The scapulae, which in the mounted skeleton are positioned too low in the chest, have been raised to represent the highest point of the back skeleton. The sternum has been positioned more backwards to follow the profile of the chest in a more natural way. The posture of the hands has been corrected making the anterior autopods more digitigrade as observed in other fossil specimens and in extant proboscideans. The forelimbs in the mounted skeleton are too separated in the scapulae area, due to the volume occupied by the metal support structure. This could lead to a not negligible increase in volume in the anterior portion of the body, compared to the natural observed condition. The anterior limbs were then digitally isolated, and positioned closer to the body midline; with this correction, the forelimbs in dorsal view result consistently closer when compared to the hind ones, as observed in extant and fossil mounted proboscideans (see Larramendi 2015, 2016).

The software was used to reconstruct the soft part around the skeleton (Fig. 2) and to build the *in vivo* appearance of *M. meridionalis*, following as reference Morfeld et al. (2016) as an indication of fleshy volumes in natural condition, were starved or obese animals are extremely rare (same procedure followed by Romano et al. 2021b). Differently, as stressed by Morfeld et al. (2016), obese elephants characterize about 34% of zoo individuals, thus deviating from the condition found in nature.

Body mass estimate - 3D volumetric methods

The digital reconstruction was imported and scaled in the software 3D Studio Max to calculate the surface and volume, following the same procedure proposed by Romano & Manucci (2019), Romano & Rubidge (2019) and Romano et al. (2021a, 2021b, 2021c). The model was scaled in the software by using as reference the length of the four stylopods measured directly on the specimen. Once the volume was obtained, we applied three different densities to the living tissue to obtain a volumetric estimate of the body mass range in *M. meridionalis*. Generally, in several body mass estimates of extinct tetrapods a density of water equal to 1 kg/1000 cm^3 is used (e.g., Alexander 1985, 1989; Gunga et al. 1995; Henderson 1999; Hurlburt 1999; Hutchinson et al. 2007; Bates et al. 2015; Larramendi et al.

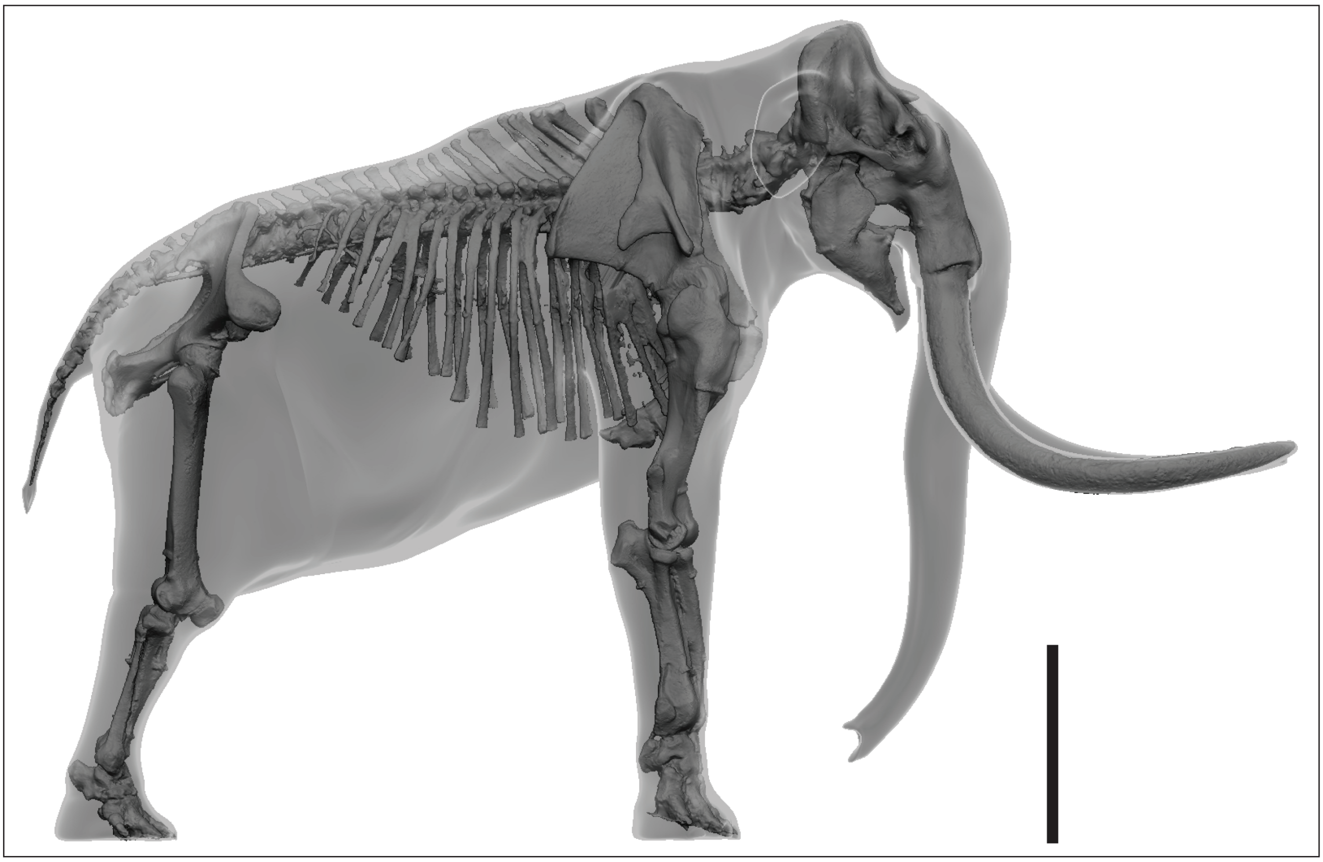


Fig. 2 - Digital sculpture in transparency around the original skeleton of *Mammuthus meridionalis* realized with the software for painting and sculpting ZBrush. Scale bar equal to 1 m.

2020; Romano et al. 2021b, 2021c). Recently, Larramendi et al (2020) showed that the vast majority of mammals have a specific gravity very close to 1.0. According to Larramendi (2016), the specific body density of extinct proboscideans ranges from 0.99 to 1.01 kg/1,000 cm^3. Based on these values proposed in the literature, in the present work we apply the three different densities of 0.99, 1.00, and 1.01 kg/1,000 cm^3 to the obtained volume in order to have a possible range of weight estimates for the studied specimen of *M. meridionalis*.

Body Mass and Shoulder Height estimate: regression equations

Various methodological approaches have been proposed by a number of authors to estimate the body mass (BM) of proboscideans. These include: regression equations resulting from measurements of selected skeletal elements from living species, formulas based on shoulder height, the graphic double integration volumetric method, and 3D *in vivo* restorations (e.g., Roth 1990; Christiansen 2004; Palombo & Giovinazzo 2005; Lister & Stuart 2010; Larramendi 2015, 2016; Larramendi & Palombo 2015; Romano et al. 2021b and references therein).

The method based on regression equations obtained from long bone linear dimensions has been largely used for predicting BM of proboscideans. Long bones do indeed support the body weight of large mammals in static and dynamic conditions and, therefore, their dimensions show good predictive consistency in estimating large mammal and pachyderm BM. The equations based on *manus* circumference proposed by Palombo & Giovinazzo (2005) for predicting the BM of the dwarf Sicilian elephant *Palaeoloxodon* ex gr. *falconeri* could hardly be applied to large sized elephants due to the difficulty of correctly estimating the cushion dimension in static position and the in-flesh *manus* circumference from bones, even in a mounted skeleton.

Consequently, we have compared the BM estimated with the 3D *in vivo* restoration with those obtained from means of log-transformed linear regression equations based on the *M. meridionalis* from MdS long bone dimensions. The latter were taken first hand directly from the specimen by using a caliper and a flexible measuring tape for circumferences.

Among the diverse predictive formulas proposed by the authors, we have chosen to calculate the BM by means of the widely employed Christiansen's (2004) regression equations, using all the available linear long bone dimensions of the MdS individual. We cannot use the regression equations proposed by Roth (1990) for elephants because the bone dimensions of the MdS mammoth largely exceed the size range over which each equation applies (Roth 1990, p. 158, Table 9.1).

Some authors attempted to predict BM of extant elephants from their stature and to formulate a function able to describe the increase in stature and BM with age in extant African (e.g., Johnson & Buss 1965; Laws 1966; Hanks 1972; Laws et al. 1975) and Asian elephants (Benedict 1936; Flower 1943; Momin Khan 1977; Lewis & Fish 1978; Tunwasor et al. 1980; Sukumar et al. 1988). Roth (1990, p.159, table 9.2) used nearly all equations of mass on shoulder height published for wild African and Asian populations of elephants for estimating the size of fossil elephants, focusing especially on insular dwarf *Mammuthus exilis* from Channel Islands (California) and the smallest endemic Sicilian and Malta elephants (*P. falconeri*). She also tested the equations on some specimens of *Mammuthus columbi* (Falconer, 1857), but found that none of the mass estimation equations were appropriate for estimating BM of such elephant, larger that the extant ones. Furthermore, inferring the BM of extinct elephants on the basis of their stature implies correctly estimating their height at the shoulder. Some authors calculated the shoulder height of mounted skeletons (sSH) at the highest point of the spines of the thoracic vertebrae above the scapula, which actually is the highest point of the back on most mounted skeletons (Christiansen 2004; Kosintsev et al. 2004; Lister & Stuart 2010; Baigusheva et al. 2011). However, Larramendi (2015, p. 539) noted that in extant walking elephants, the scapulae rises and lows several centimetres above the spines. Therefore, given the similar limb bone shape of extant and extinct Elephantinae, sSH could be measured or calculated at the top of the scapula.

Larramendi (2015, 2016) calculated sSH by either digitally restoring the fore limb in anatomical position, and multiplying by 0.98 the sum of the articular (physiological) length of the scapula, humerus, and ulna, and the manus height, or multiplying by 0.95 the sum of the maximum length of the scapula, humerus, and radius, and the manus height. The later can be estimated from the radius or III metacarpal length (Larramendi 2016, table 2, p. 540). The in flesh shoulder height (ifSH) has been estimated to be about 5.5% higher than sSH (Larremendi 2016 and references therein).

According to Larramendi (2016, table 7, p. 552), the BM of large *M. meridionalis* individuals can be estimated from the shoulder height by means of the following equation: BM (kg) = $3.08 \text{ x}^{10\text{-}3} \text{ x SH}^{2.903}$. We have obtained the stature of the MdS individual based on the 3D model (3DSH), and applied the equations proposed by Larramendi (2016) for estimating SH and ifSH, as well as for tentatively calculating BM from the stature estimates. Actually, Larramendi (2016) proposed the sSH formula for living animals. Therefore the BM value obtained using the sSH estimate has to be considered only hypothetical and is herein proposed for comparative purposes.

We also evaluated the goodness of the universal formula (LogBM = 2.754 x $\log C_{h+f}$ - 1.097) for estimating weight in tetrapods proposed by Campione & Evans (2012). The authors derived the universal regression equations from a large dataset that included mammals and non-avian reptiles, and proposed the combination of the circumferences of the femur and the humerus as the best proxy for calculating body mass in extinct tetrapods, including the largest mammals because in their dataset: "*none of the largest animals are residual outliers, including the buffalo, hippopotamus, and elephant*" (Campione & Evans 2012, p. 12).

Statistical univariate analysis (e.g., texts for testing the normal distribution of data, skewness and kurtosis) has been performed using PAST 4.0 software (Hammer et al. 2001).

Results

In vivo restoration and BM estimate

The 3D model of *M. meridionalis* based on the specimen on display at the east bastion of the Spanish Fortress at L'Aquila was reconstructed by adding a mass of fleshy parts as close as possible to the natural condition (see Morfeld et al. 2016), and adhering the body contours of extant elephants (Figs.

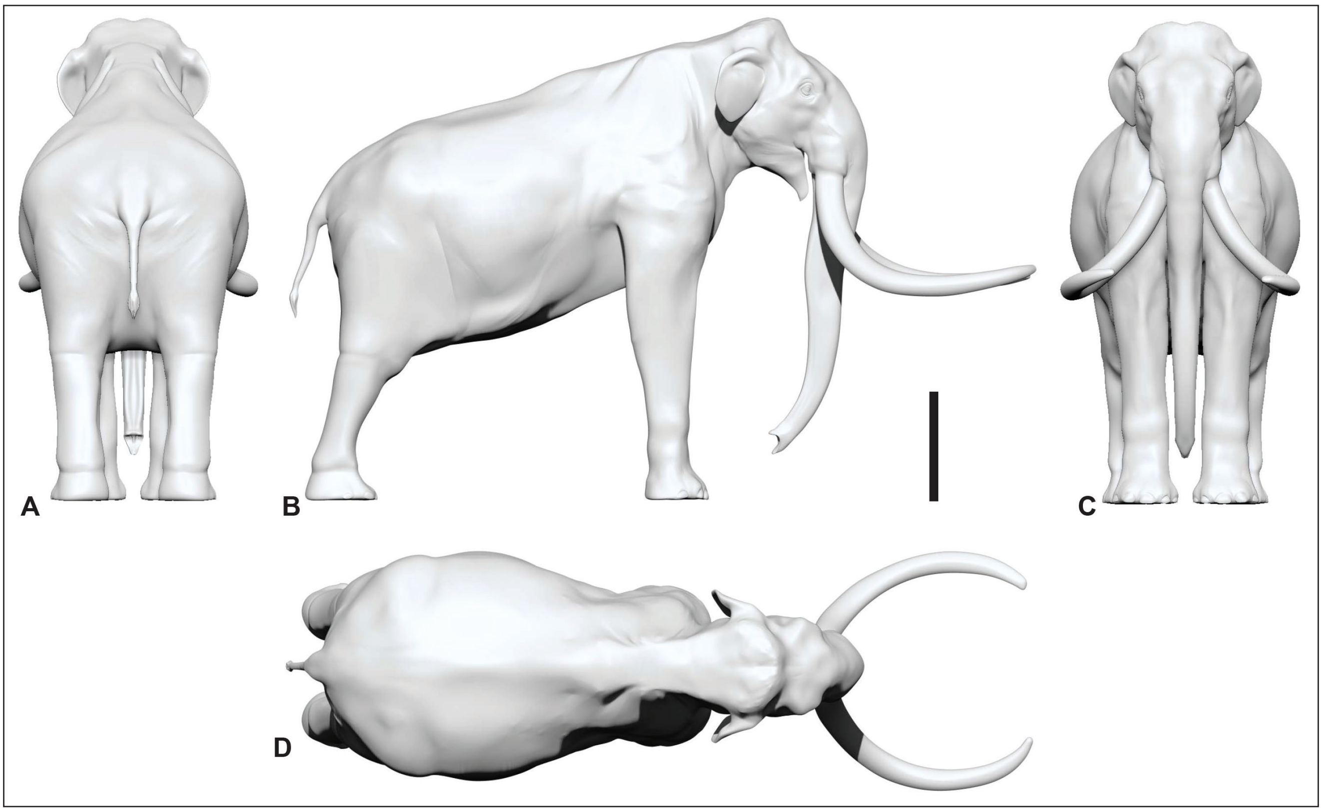


Fig. 3 - Solid model of *M. meridionalis* in posterior (A), lateral (B), frontal (C) and dorsal (D) views. Scale bar equal to 1 m.

2, 3). The model produced a total area of 48.63 square meters and a total volume of 11.43 m^3 when the tusks were included. The volume was, indeed, calculated with both tusks in physiological position, although the left tusk was lost during the animal's life (Della Salda et al. 2016). By applying the densities of 0.99, 1, and 1.01 kg/1,000 cm^3 to the reconstructed *in vivo* volume, we obtained a body mass range of 11.3, 11.43 and 11.5 tons, respectively. The *in vivo* restoration of *M. meridionalis* is shown in Figure 4.

Body mass and shoulder height estimates: regressions equations

The BM estimates of the MdS mammoth, obtained from using the available left and right long bone measurements among those suggested by Christiansen (2004), show a large variation range. The mammoth BM ranges from 1,284 kg to 38,300 kg, with an average BM estimate of about 14,981 kg (Tab. 1, 2) that definitely exceeds any other estimate already obtained for *Mammuthus* representatives (e.g., Christiansen 2004; Larramendi 2015, 2016, and references therein). The summary of statistical data highlights the high coefficient of variation (52.33), which is significantly higher than the maximum value (20.0) for considering it acceptable, and the p value of the Jarque-Bera text for normality is < 0.05, rejecting the null hypothesis of normally distributed data, but it is > 0.05 in the Shapiro-Wilk and Anderson-Darling, suggesting a normal distribution of data. The "not-normal" distribution of data, is partially supported by the skewness and kurtosis indices, both reflecting some deviation from normality, being moderately asymmetric and right long-tailed due to the presence of particularly high BM values (Tab. 2).

In the box plot obtained from considering all BM estimates (sample A) (Fig. 5A), BM obtained from the lateral condyle length of the femur (F-lcl) measurements falls above the upper inner fence, which corresponds to the largest data point less than 1.5 times the box height (outliers), whereas the BM obtained from the lateral (H-lcl) and medial (H-mcl) condyle length of humerus measurements are the highest among the other BM estimates. The BM values obtained from the circumference of the humerus (H-circ.) and ulna (U.circ.) roughly match the average (14,981 kg) and median (14,955 kg). Conversely, the lowest BM values (at the bottom

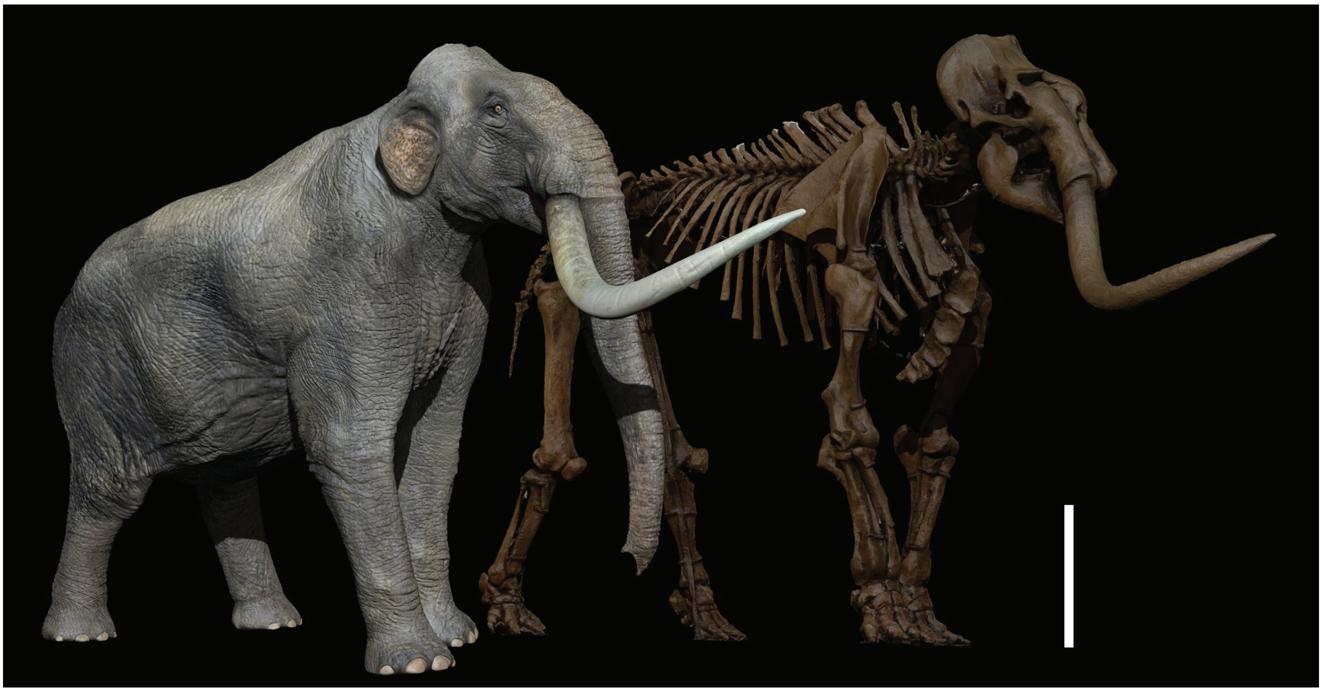
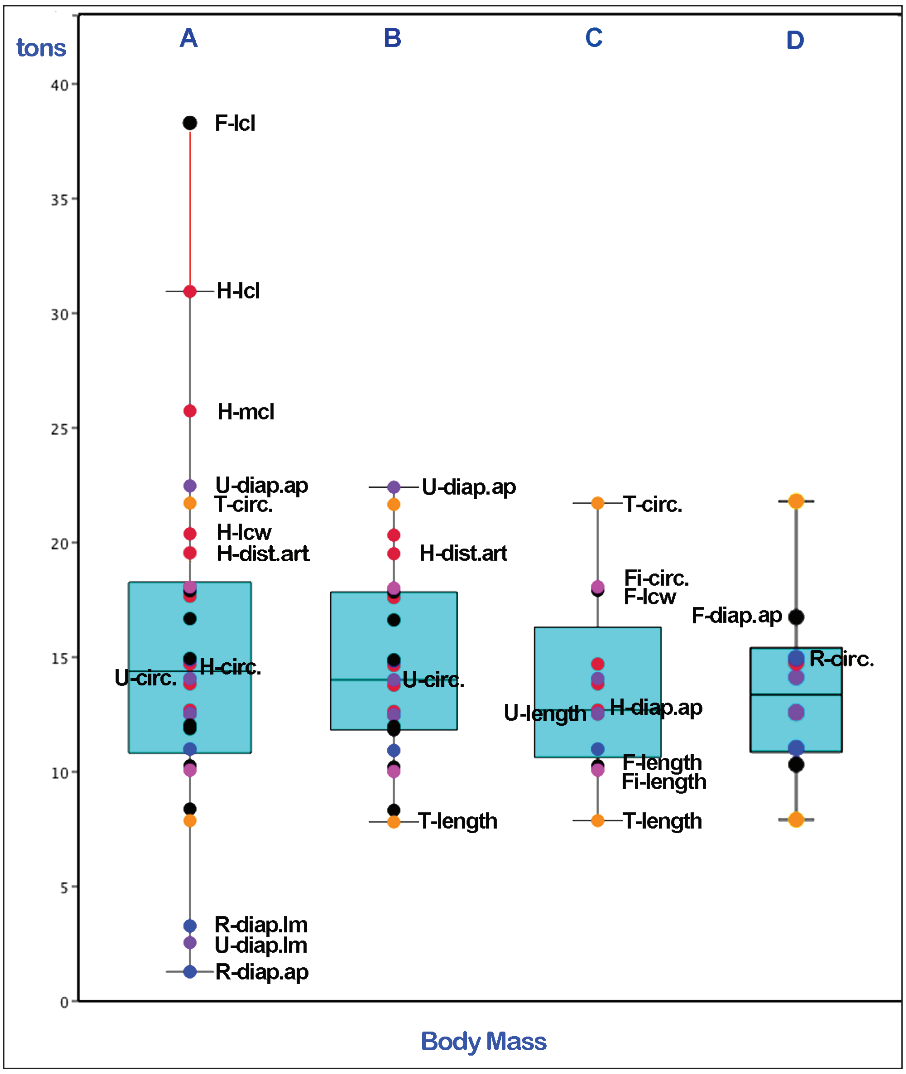


Fig. 4 - Photogrammetric reconstruction of the skeleton (right) and *in vivo* restoration of *M. meridionalis* (left). Scale bar equal to 1 m.

Fig. 5 - Box plot illustrating the variation range of body mass estimates for *Mammuthus meridionalis* from Madonna della Strada. BM was calculated by averaging the BM obtained by measuring the left and right sides of the long bones. A) sample including the BM estimates obtained from all of the available measurements, among those suggested by Christiansen (2004). B) sample excluding the BM value of sample A considered unrealistic for any adult elephant male; c) sample excluding the BM obtained from the regression equations with the lowest percent standard error of the estimate (%SEE) and percent prediction error (%PE). Abbreviations: F = femur; Fi = fibula; H = humerus; R = radius; T = tobia = U = Ulna; 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.



Mammuthus meridionalis - Madonna della Strada - Scoppito (L'Aquila)														
Variable	a±95% CI	b±95% CI	r	%SEE	%PE	Long Bone measurements (mm)		Measurements - logarithm base 10		BM (logarithm base 10)		Estimated Body Mass (Kg)		
						left (L)	rigth (R)	left	rigth	left	rigth	left	dx	(L+R)/2
HUMERUS														
Humerus length	-4,1450	2,6350	0,9900	11,5200	6,7400	1350	1350	3,1303	3,1303	4,1034	4,1034	12689	12689	12689
Humerus circ.	-1,5980	2,0620	0,9950	7,7800	5,5400	640	610	2,8062	2,7853	4,1883	4,1454	15429	13975	14702
Humerus diap.ap	-0,5030	2,0090	0,9970	5,9700	3,6200	195	195	2,2900	2,2900	4,0977	4,0977	12522	12522	12522
Humerus diap.lm	-0,6600	2,1240	0,9890	12,2100	8,5600	189	175	2,2765	2,2430	4,1752	4,1042	14969	12712	13841
Humerus dist.art	-5,2900	3,8720	0,9600	24,3300	16,7200	310	285	2,4914	2,4548	4,3566	4,2152	22728	16412	19570
Humerus mcl	-2,5540	2,9430	0,8810	43,1500	28,3400	235	230	2,3711	2,3617	4,4241	4,3966	26549	24921	25735
Humerus mcw	-3,2020	3,4090	0,9440	29,0900	18,5100	130	170	2,1139	2,2304	4,0044	4,4016	10103	25212	17657
Humerus lcl	-2,2940	2,8670	0,9040	39,3400	25,4300	235	230	2,3711	2,3617	4,5039	4,4771	31904	29997	30951
Humerus lcw	-3,7840	3,7750	0,7520	66,5800	39,6100	120	153	2,0792	2,1847	4,0649	4,4646	11612	29149	20381
Humerus-average BM												**18227**	**20612**	**18672**
RADIUS														
Radius length	-3,8380	2,6340	0,9920	10,1100	6,6400	980	-	2,9912	-	4,0409	-	10987	-	10987
Radius circ.	-0,7540	2,0010	0,9720	20,0400	12,3000	290	-	2,4624	-	4,1733	-	14902	-	14902
Radius diap.ap	-0,4300	1,8340	0,9580	24,9100	15,3100	85	-	1,9294	-	3,1086	-	1284	-	1284
Radius diap.lm	-0,3510	1,9690	0,9600	26,0100	16,3000	92	-	1,9638	-	3,5157	-	3279	-	3279
Radious-average BM												**7613**		**7613**
ULNA														
Ulna length	-4,1350	2,6740	0,9950	8,4100	5,3400	-	1200	-	3,0792	-	4,0987	-	12553	12553
Ulna circ.	-1,3490	2,0220	0,9970	5,7800	4,4200	495	550	2,6946	2,7404	4,0995	4,1920	12575	15560	14067
Ulna diap.ap	-0,8720	2,3040	0,9740	19,1600	11,7900	185	-	2,2672	-	4,3516	-	22468	-	22468
Ulna diap.lm	-0,1850	1,7430	0,9920	10,4800	7,8800	115	135	2,0607	2,1303	3,4068	3,5282	2552	3374	2552
Ulna-average BM												**12531**	**10496**	**12910**
FEMUR														
Femur length	-5,5680	3,0360	0,9850	14,5400	6,1500	1420	1440	3,1523	3,1584	4,0023	4,0208	10054	10490	10272
Femur circ.	-1,6060	2,0730	0,9760	18,4600	11,5200	550	550	2,7404	2,7404	4,0748	4,0748	11879	11879	11879
Femur diap.ap	-0,9120	2,3150	0,9800	16,6400	11,4000	170	160	2,2304	2,2041	4,2515	4,1905	17844	15507	16676
Femur diap.lm	-0,3420	1,9040	0,9660	22,2300	14,4200	402	406	2,6042	2,6085	4,6164	4,6246	41347	42134	41741
Femur dist.art	-4,3470	3,5020	0,9280	33,4900	21,7100	255	-	2,4065	-	4,0807	-	12042	-	12042
Femur mcl	-0,8190	2,1560	0,8620	23,4200	15,3500	207	-	2,3160	-	4,1742	-	14936	-	14936
Femur mcw	-1,5500	2,6190	0,9500	27,3900	17,7100	123	-	2,0899	-	3,9235	-	8384	-	8384
Femur lcl	-4,9700	4,3450	0,8330	53,4900	30,9800	158	-	2,1987	-	4,5832	-	38300	-	38300
Femur lcw	-1,5140	2,6950	0,9870	13,2100	9,9100	138	-	2,1399	-	4,2530	-	17905	-	17905
Femur-average BM												**20330**	**23173**	**19126**
TIBIA														
Tibia length	-3,0640	2,3780	0,9880	12,4700	6,9300	850	840	2,9294	2,9243	3,9022	3,8899	7982,8543	7761	7872
Tibia circ.	-2,7240	2,6470	0,9910	10,7200	6,5700	460	470	2,6628	2,6721	4,3243	4,3490	21102	22338	21720
Tibia diap.ap	-1,0440	1,3950	0,9730	19,4600	13,7100	138	125	2,1399	2,0969	1,9411	1,8812	-	-	-
Tibia diap.lm	-0,9500	1,3910	0,9700	20,8200	14,1200	148	160	2,1703	2,2041	2,0688	2,1159	-	-	-
Tibia-average BM												**14542**	**15050**	**14796**
FIBULA														
Fibula length	-3,0860	2,4220	0,9750	18,6800	11,4000	840	850	2,9243	2,9294	3,9966	5,2782	9922	10212	10067
Fibula circ.	-0,4830	2,0970	0,9930	9,5700	6,2400	170	170	2,2304	2,2304	4,1943	4,3118	15641	20504	18072
Fibula diap.ap	-1,6950	1,2630	0,9590	24,6200	17,3100	-	-	-	-	-	-	-	-	-
Fibula diap.lm	-2,0200	1,2150	0,9320	32,3800	19,9700	-	-	-	-	-	-	-	-	-
Fibula-average BM												**12781**	**15358**	**14070**

Tab. 1 - Body Mass (BM) estimates of *Mammuthus meridionalis* from Madonna della Strada-Scoppito calculated using the following Christiansen's (2004) formala : log (BM)= a+b(logX) X=bone variables. 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. * Average value obtaining by removing the highest BM estimated.

of the 1st percentile, which includes all values below the box), obtained using the radius (R-diap.lm) and ulna (U.diap.lm) diaphysial medio-lateral width, and radius diaphysial antero-posterior width (R-diap.ap) are unrealistically low (less than 3,300 kg, Tab. 1) for an adult elephant male.

With the purpose of obtaining more compelling results, we have performed a new analysis after removing the outliers and the lowest-value estimates. The values of the 23 selected BM (sample B) range from 7,870 kg to 21,720 kg. The highest and lowest BM values are those obtained respectively from the ulna diaphysial antero-posterior width (U-diap. ap) and tibia length (T-length). The obtained box plot (Fig. 5B) shows that the average BM value is a little lower (14,616 kg) than that resulting from the previous analysis, whereas the median is lower (14,072 kg), matching the BM value obtained from the ulna circumference (U-circ.). The skewness and kurtosis indices indicate a limited asymmetry. The normality texts show a p-value > 0,05, and the coefficient of variation is notably lower than that resulting from the analysis of all the BM estimates. Although it is still moderately high (28.09), it is, however, < 30 and, therefore, acceptable.

It is worth noting, however, that several BM values have been obtained by applying regression equations that have a per cent standard error of

Summary Statstics - BM in t)				
	Sample A	Sample B	Sample C	Sample D
N	30	23	13	12
Min	**1284**	**7870**	**7870**	**7870**
Max	**38300**	**22468**	**21720**	**21720**
Sum	449426	323923	177274	164412
Mean	**14980.67**	**14615.65**	**13636.46**	**13701**
Std. error	1.431266	0.8560897	1.050836	1.114144
Variance	61.45564	16.85646	14.35532	14.89581
Stand. dev	7.839365	4.105.662	3.788842	3.85509
Median	**14955**	**14073.2**	**12690**	**13311.5**
25 prcntil	1081	11883	10628,5	10449.25
75 prcntil	18445	17988	16306	16232.5
Skewness	0.9106625	0.311874	0.7194632	0.6043846
Kurtosis	1.885252	0.2721559	0.3815032	0.3038068
Geom. mean	12554.77	14058.38	13171.03	13214.73
Coeff. var	**52.32988**	***26.96006***	***27.78464***	***28.16954***

Normality Test				
	Sample A	Sample B	Sample B	Sample D
N	30	23	13	12
Shapiro-Wilk W	0.9411	0.9679	0.9507	0.9711
p(normal)	**0.09756**	**0.6395**	**0.6083**	**0.9224**
Anderson-Darling A	0.5861	0.2605	0.3336	0.1915
p(normal)	**0.1179**	**0.6774**	**0.4551**	**0.8696**
p(Monte Carlo)	**0.122**	**0.6899**	**0.4704**	**0.8855**
Lilliefors L	0.1354	0.1207	0.1585	0.1278
p(normal)	0.1665	0.5097	0.4886	0.8479
p(Monte Carlo)	0.1665	0.5132	0.4964	0.8497
Jarque-Bera JB	6.158	0.9489	0.8872	0.59
p(normal)	**0.046**	**0.6222**	**0.6417**	**0.7445**
p(Monte Carlo)	**0.029**	**0.4662**	**0.4105**	**0.6234**

Tab. 2 - Statistical summary and normality texts results obtained for the samples A, B, C, and D (A,B,C, and D as in Figure 1).

the estimate (%SEE) and a per cent prediction error (%PE) that are either high or noticeably high (e.g., %SEE > 26.00, and %PE > 16.00), and often have a rather low value of correlation coefficients (r < 0.95). So that, the corresponding predicted BM values deviate significantly from the regression line. As a result, the predictive power of these regression equations is very low and the corresponding BM estimates may be improbable, especially given that %SEE and %PE permit evaluating the predictive power of a regression equation better than r. Consequently, we have ordered and grouped the BM estimates, based on the %SEE and %PE of the equations from which they were generated (Tab. 3).

The variation range of the sample of the 13 BM values of groups A and B (sample C), characterised by the lowest %SEE (< 15) and %PE (< 10), and the highest r (> 0.98) (Tabs. 1, 3), is still rather large (2,522-21,720 kg) due to the relatively low values of %PE and %SEE of the regression predictive equations of the tibia circumference (%PE 0 6.57; %SEE = 10.72) and the ulna diaphysial latero-medial width (%PE 0 7.88; %SEE = 10.48) (Group B) that respectively generated the highest (21,720 kg) and the lowest BM estimate (7,872 kg) of the sample. The BM values obtained from the four equations with the lowest %PE and %SEE (Group A: humerus diaphysial antero-posterior width and circumference, and ulna circumference and length) range from 12,522 kg to 14,702 kg, with an average value of 13,461 kg, whereas that of Group B is rather lower (12,879 kg) due to the very low BM value (2,552 kg) mentioned above. Since this estimate is unrealistic for any adult elephant, we statistically analysed the sample without considering the value.

The range of the BM values obtained from the measurements included in sample C (7,872 kg-21,720 kg) is almost the same as that of sample B, but the average BM is lower (13,636 kg) as it is the median (12,690 kg). The BM estimates obtained by the humerus diaphysial antero-posterior width and the ulna length are the closest to the median value (Figure BM1C). The coefficient of variation (27.784) is acceptable. The curve is a little more asymmetric than that of sample B, and right-tailed. The p-value of normality texts is more than the significance level. Therefore, the null hypothesis is verified and the data follow a normal distribution (Tab. 2).

The regression equations considered in sample C are nearly the same as those regarded by Christiansen (2004, p. 529) as the best predictive for individual bones, with the exception of the equations based on the length and diaphyseal mediolateral width of the humerus, and the femur lateral condyle width, but including the radius circumference and the femur diaphyseal antero-posterior width (Fig. 5). The range of the corresponding BM estimates (sample D) and the average BM values are roughly the same as those of sample C. The median BM value is slightly higher (13,311 kg) as it is the coefficient of variation (28.1695), but the curve is less asymmetric (Tab. 2).

All things considered, the statistic parameter may suggest that the BM estimates in the sample C are the most compelling, and that the predicted BM average estimate (about 13,600 kg) may be hypothesised as the most suitable for the MdS mammoth. The BM value is just fairly larger, but roughly comparable with that obtained by Larramendi (2016, table 4, p. 542) (13,207 kg) by using Christiansen's (2004) equations for the bones parameters with low

Group	r		%SEE		%PE		Body Mass (Kg)	
	Value	Range	Value	Range	Value	Range	M	Range
A	> 0.995	0.995-0.997	< 10	5.97-7.78	< 6	3.62-5.54	13461	12522-14702
B	> 0.980	0.985-0.992	< 15	9.57-14.54	< 10	6.15-9.9	12879	2552-17905
C	> 0.987	0.972-0.980	< 21	16.64 -20.04	< 14	11.4-13.71	15198	10067-22468
D	> 0.949	0.950-0.970	< 28	22.23-27.39	< 14	14.12-17.71	9148	1284-19570
E	> 0.750	0.75-0.9440	< 67	29.09-66.58	< 40	18.51-39.61	24178	12042-38300

Tab. 3 - Groups formed including the BM estimates ordered according to the increasing value of the per cent standard error of the estimate (%SEE) and per cent prediction error (%PE).

prediction error (PE%<15) among those available in Maccagno (1962).

The two heights at the shoulder of the MdS mounted skeleton (sSH), obtained by summing either the maximum (sSH1) or the physiological (sSH2) length of the scapula and long bones, plus the manus height (Larramendi 2016) (all elements were measured directly on the specimen), are nearly the same (Tab. 4), with an average skeleton stature of 383.5 cm. The corresponding flesh stature (ifSH) is almost 4 m (404.6 cm), just fairly higher than the stature (397 cm) obtained by Larramendi (2016) by using Maccagno's (1962, table 31, p 94) measurements. The BM value estimated from ifSH (11,396 kg) is inferior to the average values obtained from the measurement of long bones. The inferred in-flesh height at the shoulder measured on the 3D model (ifSH 3D, 9,926 kg) is even lesser (Tab. 4), as it is with respect to the BM obtained by the volumetric method by Larramendi (2016) (10,744 kg), roughly comparable with that herein obtained from the ifSH estimate.

SHOULDER HEIGHT (cm)				**BODY MASS** (kg)
maximum lenght		physiological length)		
Scapula	117	Scapula	115	
Humerus	135	Humerus	125	
Radius	100	Ulna*	98	
Manus Height**	52	Manus Height	52	
SH 1	384	SH 2	383	
***sSH** =(SH1+SH2)/2 (1)*	***383.5***			***9672***
ifSH	**404.6**			**11396**
sSH 3D (1)	**375**			***9130***
ifSH 3D	**395.6**			**9926**

Tab. 4 - Height at the shoulder and BM estimates in the mounted skeleton of *Mammuthus meridionalis* from Madonna della Strada and in the 3D model, calculated by applying the methods proposed by Larramendi (2015, 2016). * = measurements taken on the right ulna; ** = high manus estimate is based on the third metacarpal length (III MC L) (manus H = III MC L x 2) (Larramendi, 2016); sSH = skeletal shoulder height; ifSH = in-flesh shoulder height. (1) The sSH and relative BM estimate, obtained by applying the Larramendi's (2016) equation, have to be considered hypothetical because we attempt to calculate sSH from the skeleton bone measurements and the 3D model of a fossil specimen, whereas such an equation was proposed only for estimating shoulder height in living individuals.

The application of the formula proposed by Campione & Evans (2012) on both left and right stylopods returned an average BM of 21,662 kg, with a minimum of 16,247 kg and a maximum of 27,078 kg, considering the +/- 25% error proposed by the authors. Thus, the regression formula overestimates the BM compared to our volumetric estimate from a minimum of 42% to a maximum of 137%.

All things considered, according to the BM estimates obtained by using the Christiansen (2014) regression equations, as well as those resulting from the application of the SH formulas, and the application of the 3D volumetric method, the hypothesis that the MdS mammoth might weight between 11,000 kg and 13,500 kg seems to be the most reasonable, though indicative despite the wide range of values obtained.

Discussion

Estimating the BM of extinct tetrapods represents a very important field of research, allowing several crucial inferences at the biological level, and playing a central role in the reconstruction of macroevolutionary processes. The size of a taxon within a clade, and its evolution over time, can have repercussions and allow inferences in various aspects of the biology of extinct animals, including growth rate, general metabolism, ecology, trophic requirements, home range, fecundity, life span and reproduction rate, among several others (e.g., Millar & Zammuto 1983; LaBarbera 1989; Martin & Palumbi 1993; Calder 1996; Hillebrand & Azovsky 2001; Angiletta et al. 2004; Davidowitz & Nijhout 2004; Nagy 2005; Gillooly et al. 2006; Fisher et al. 2011; Campione & Evans 2012; Clauss et al. 2013). It is therefore of primary importance to recognize such methods and approaches that allow to obtain sound an plausible body mass estimates in extinct vertebrates, in any case as close as possible to natural conditions.

In this framework, the results obtained in the present study and showed in a comparative way in

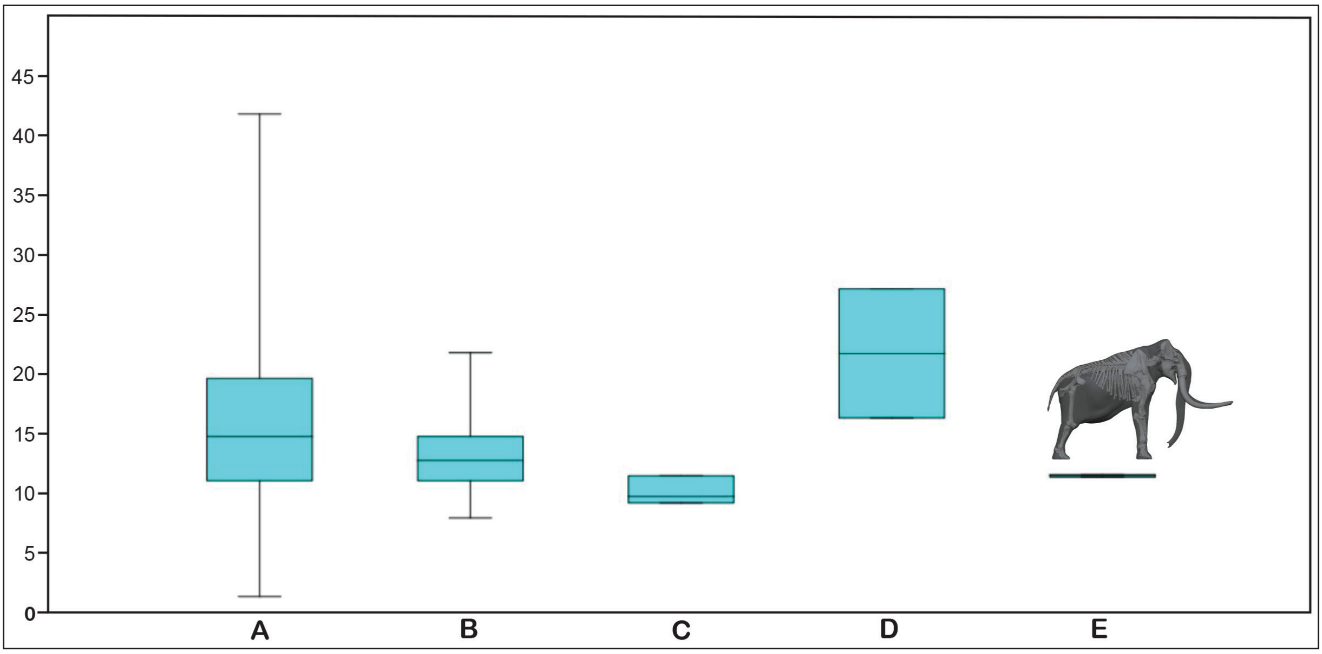


Fig. 6 - Box plots relating the ranges of the BM estimate obtained with the volumetric method and with traditional regression methods. A) Estimate with Christiansen's (2004) regression equations using all measurements (sample A) ; B) estimate with Christiansen's (2004) regression equations using selected measurements (sample C); C) estimate from the high at the shoulders calculated with the Larramendi's (2016) formulas (see Table 4); D) estimate with regression equations proposed by Campione and Evans (2012); E) estimated based on the volumetric method presented in this contribution.

Figure 6, allow us to make some interesting general considerations.

In this paper we presented an *in vivo* reconstruction of *Mammuthus meridionalis* starting from a 3D photogrammetric model of a mounted skeleton. The 3D model was obtained by adding to the skeleton a percentage of soft tissues in accordance with the conditions observed in wild specimens (following Morfeld et al. 2016) (Fig. 3). The volume calculated from the model was also utilized to obtain an estimate of the BM of the adult male specimen, applying the density range proposed for the proboscideans by Larramendi (2016). The BM estimated on a volumetric basis returned a minimum value of 11.3 t and a maximum of 11.5 t, with a BM average equal to 11.41 t. Since volumetric calculation of BM in extinct tetrapods performs better and returns more plausible estimates, as empirically shown in several contributions (e.g., Sellers et al. 2012; Bates et al. 2015; Brassey et al. 2015; Larramendi 2016; Romano & Manucci 2019; Romano & Rubidge 2019a; Romano et al. 2021a, 2021b, 2021c), the values obtained with the 3D model were used as a reference to discuss the estimates calculated with the classical regression formulas proposed in the literature (i.e., Christiansen 2004; Campione & Evans 2012; Larramendi 2016).

The comparison between the weight estimates obtained through the volumetric method and the ranges of the values obtained applying the classic regression formulas, based both on individual osteological element dimensions, and on the mounted specimen shoulder height (Fig. 6) highlights the inconsistency of the BM values resulting from the latter.

The values obtained using Christiansen's (2004) formulas show the widest range of estimates, with values ranging from a minimum of only 1.20 tons to a maximum of almost 42 tons (Fig. 6A). The results obtained by using only the Christiansen's (2004) formulas with the lowest %SEE (< 15) and %PE (< 10) and the highest r (> 0.98) (sample C), show a much more limited range (Fig. 6B). The values of the BM estimate range from a minimum of about 8 t to a maximum of about 22 t, which is decidedly more plausible having the volumetric estimate as reference.

The values obtained with the method based on the shoulder height proposed by Larramendi (2016) show a much more restricted range (Fig. 6C), especially considering that the minimum of about 9 tons was calculated on the height of the skeleton based on a 3D model, applying a formula originally not intended for mounted skeletons of fossil specimens. The BM value of about 11 tons, calculated by considering the fleshy part covering the skeleton, is inferior to the BM estimated by both the allometric and the 3D model volumetric methods. (Fig. 6), and it is very close to the average value obtained in the present work equal to 11.41 t.

The method proposed by Campione & Evans (2012) always leads to an overestimation of the BM (Fig. 6D) as already highlighted in other contributions (e.g., Romano & Manucci 2019; Romano & Rubidge 2019a; Romano et al. 2021b, 2021c). In particular, the obtained values range from a minimum of about 16 tons (above the maximum limit of the volumetric method), to a unlikely maximum of about 27 tons (Fig. 6D).

Although the results obtained for reduced sample (sample C) with Christiansen is (2004) formulas show a fairly wide range, the average estimate 13.6 tons, is only 19% higher than the volumetric estimate. This indicates that the measurements reported for sample C, when considered together on average, can provide a quite reasonable BM estimate at least for the genus *Mammuthus*. As a result, these regression formulas can be employed to get acceptable weight estimates in the case of substantially complete skeletons, if a mounted skeleton is not available to obtain a volumetric BM estimation. Conversely, the results obtained using all the regression formulas proposed by Christiansen (2004) (Figure 5A) clearly indicate that the BM estimates based on a single, maybe fragmentary, bone can be extremely misleading, resulting in severe overestimates or underestimates of proboscidean body weight. The radius diaphysial diameter in the anteroposterior plane, which provides an estimate of only 1.28 tons, and the length of the femur lateral condylus, which provides extremely high values of more than 38 tons for a specimen more than 4 meters tall, are emblematic examples in the case of the MdS mammoth (Table 1). Otherwise, the estimates based on femur circumference (11.88 t), femur width of distal articular surface (12.04 t), humerus diaphysial diameter in the anteroposterior plane (12.52 t), ulna length (12.55 t) and humerus length (12.69 t), come closest to the estimate base on the volumetric method (11.41 t). It is interesting to note that the BM value calculated with the formulas by Christiansen (2004) on the sample C is rather equal to the average BM obtained averaging the values based on the humerus circumference and diaphysal anteroposterior width (13,461 kg), and the ulna length and circumference (group A), which includes the regression equations with the best %PE and %SEE (Tabs. 1, 3). The datum may support the hypothesis of the major loading the forelimb bones have to support in elephants.

Finally, the method proposed by Larramendi (2016), based on the skeleton and in-flesh heights at shoulder measured on the 3D model and on the mounted skeleton, provides a mean value that is totally congruent with the volumetric weight estimate, even if a 6% lower on average. Conversely, the formulas proposed by Campione & Evans (2012) always result in a overestimation, of the BM, with an average value calculated 90% higher than the volumetric method one with, and a maximum value of more than 27 tons (137% higher than the volumetric estimate), calculated with the formula based on the circumference of the humerus. The presence of 'overbuilt' long bones (*sensu* Romano 2017; Romano & Rubidge 2019b) in extinct vertebrates and their absence in extant taxa selected by Campione & Evans (2012) to construct the regression formulas could explain that overestimation. This seems to be precisely the case with the long bones in *Mammuthus meridionalis*, especially the anterior ones, which could depend on the major BM loading on the forelimb bones than on the posterior ones in proboscideans (especially in male individuals).

Conclusions

In conclusion, the estimate of the BM of 11.41 t obtained applying the volumetric method to a mounted skeleton of *M. meridionalis* seems to be the most reasonable. The results obtained confirm that the volumetric method is always preferable if sufficiently complete mounted skeletons are available. In the case of mounted skeletal remains of fossil taxa sensibly different in proportions to their extant relatives, it is recommended to reconstruct various amounts of fleshy tissues around the skeleton, as already proposed by some authors (Romano & Manucci 2019; Romano & Rubidge 2019a; Romano et al. 2021c), in order to have a possible range of volume and, in turn, of BM. In the specific case of proboscideans or vertebrates with reasonably close extent analogues, it is suitable to assume a quantity of soft tissues as close as possible to the natural condition, given that obese or severely starving animals are generally rare in the wild.

Furthermore, the results we have obtained suggest that, in the absence of a mounted full skeleton, regression formulas for weight estimation based on single or fragmentary bones should be used with extreme caution, as they run the risk of producing severely erroneous and misleading results. The present contribution shows that for the genus *Mammuthus*, the average of the various estimates obtained from single bones applying formulas specifically obtained for proboscideans leads to a sufficiently congruent BM estimates. In general, weight estimates based on single measures and single bones should be avoided, especially dealing with groups morphologically and phylogenetically distant from extant reference taxa.

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