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Body mass estimate of *Anancus arvernensis* (Croizet and Jobert 1828): comparison of the regression and volumetric methods

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ABSTRACT: In this contribution, we estimate the possible living body mass (BM) of the anancine gomphotheriid *Anancus arvernensis*, by testing a recently proposed volumetric method based on hyper-realistic *in vivo* 3D reconstructions and comparing the results with the BM obtained by using regression formulas. The analysis, conducted starting from two articulated skeletons, showed that the performance of regression formulas varies considerably from taxon to taxon, with plausible estimates obtained only when the mean of all the formulas on the individual bones is available and considered. Differently, formulas applied to single bones can lead to underestimations or overestimations of up to 300%, with BM ranging from 54 kg to 26 metric tonnes. By using the volumetric method, the *in vivo* reconstruction of *Anancus arvernensis* made it possible to estimate a BM between 5.2 and 6 t, a figure close to that of an extant adult male African elephant. The obtained results show that estimating BM in terrestrial tetrapods from single or fragmented bones might lead to highly improbable and misleading conclusions. Thus, in the presence of adequately complete mounted skeletons, it is always preferable and recommended to estimate the BM using the volumetric approach, which is based on an *in vivo* 3D reconstruction.
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KEYWORDS: body mass estimate; digital sculpture; photogrammetry; Pleistocene; Quaternary regression formulas

INTRODUCTION

Body mass (BM) is one of the most important characteristics of both living and extinct organisms, influencing many biological aspects such as metabolism, lifespan and reproduction, fecundity, biomechanics, general ecology, dependence on the external environment, trophic requirement and diet, home range and growth rate (e.g. Millar and Zammuto, 1983; LaBarbera, 1989; Martin and Palumbi, 1993; Calder, 1996; Hillebrand and Azovsky, 2001; Angiletta et al., 2004; Davidowitz and Nijhout, 2004; Nagy, 2005; Gillooly et al., 2006; Brose, 2010; Fisher et al., 2011; Campione and Evans, 2012; Clauss et al., 2013; Brassey, 2016). As a result, a reliable estimate of the BM is a critical indicator for interpreting the palaeobiology of fossil taxa, capable of shedding light on numerous aspects at both the micro and macro-evolutionary scale (e.g. Maurer et al., 1992; Alroy, 1998; Burness et al., 2001; Smith et al., 2010; Zanno and Makovicky, 2013; Benson et al., 2014; Grabowski et al., 2015; Price and Hopkins, 2015; Puttick and Thomas, 2015). Since the last century, numerous methodologies and approaches have been developed to estimate this parameter in extinct organisms, which can be divided into two main categories: (i) regression methods, where skeletal lengths or circumferences in osteological elements are related to an organism's weight (e.g. Alexander et al., 1979; Anderson et al., 1985; Damuth and MacFadden, 1990; Roth, 1990; Ruff et al., 1991; Aiello and Wood, 1994; Wroe et al., 2003; Christiansen, 2004; Palombo and Giovinazzo, 2005; Spocter and Manger, 2007; Lister and Stuart, 2010; Campione and Evans, 2012; Field et al., 2013; Campione et al., 2014; Larramendi and Palombo, 2015); and (ii) volumetric methods, where a specific density (or range of densities) for living tissues is applied to a volume that can be estimated according to different approaches (e.g. Gregory, 1905; Colbert, 1962; Bramwell and Whitfield, 1974; Farlow et al., 1995; Gunga et al., 1995, 1999, 2008; Henderson,1999; Hurlburt, 1999; Christiansen and Paul, 2001; Mazzetta et al., 2004; Hutchinson et al., 2007, 2011; Bates et al., 2009a, 2015; Mallison, 2010; Sellers et al., 2012; Brassey and Sellers, 2014; Brassey and Gardiner, 2015; Romano et al., 2021a).

The most commonly used method to predict the BM of most fossil mammals, including proboscideans, is based on regression equations derived from long-bone linear dimensions. Long bones are responsible for supporting the body weight of large mammals in both static and dynamic conditions. Therefore, their dimensions should generally provide reliable estimates of the BM of large mammals and pachyderms.

Some authors attempted to predict the BM of extant elephants based on their stature and to develop a function that could describe the increase in stature and BM with age in extant African (e.g. Johnson and Buss, 1965; Laws, 1966; Hanks, 1972; Laws et al., 1975) and Asian elephants (Benedict, 1936; Flower, 1943; Momin Khan, 1977; Lewis and Fish, 1978; Tumwasorn et al., 1980; Sukumar et al., 1988). Roth (1990, p. 159, Table 9.2) tested almost all the published equations for estimating the BM of extant wild African and Asian elephants on some specimens of *Mammuthus columbi* but found that none of the equations were appropriate for estimating the BM of such elephants, which are larger than the extant ones.

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Various authors have proposed diverse methods for estimating BM from the height at the shoulder (sSH) of extinct mammalian species based on the dimensions of their forelimb long bone and manus in a static position. Some authors have suggested calculating the sSH of proboscidean skeletons, assuming that it could correspond to the highest point of the spines of the thoracic vertebrae above the scapula (e.g. Christiansen, 2004; Kosintsev et al., 2004; Lister and Stuart, 2010; Bajgusheva et al., 2011). However, Larramendi (2015, p. 539) noted that in extant walking elephants, the scapula rises and lowers several centimetres above the spine. Therefore, sSH could be measured or calculated at the top of the scapula due to the similar limb bone shape of extant and extinct Elephantinae. Larramendi (2015, 2016) calculated the sSH of Elephantidae representatives either by digitally restoring the forelimb in its anatomical position or by multiplying by 0.98 the sum of the articular (physiological) lengths of the scapula, humerus, ulna and the manus height, or by multiplying by 0.95 the sum of the maximum length of these bones. Conversely, for the Gomphotherioidea, where the forelimbs are slightly more flexed, the sum of forelimb bone articular length and maximum length must be multiplied by 0.97 and 0.94, respectively.

Recent studies have demonstrated that, for terrestrial tetrapods, volumetric methods outperform linear regression methods in estimating BM. Volumetric methods provide BM values that are more realistic and closer to actual conditions, and they also offer much narrower estimation ranges (Romano et al., 2022b and references therein). In several cases, the regression estimates based on limb-bone measurements resulted in very consistent overestimations of the BM, related to the fact that in several extinct tetrapods long bones are very robust ('overbuilt' *sensu* Romano, 2017; Romano and Rubidge, 2019a), in comparison to the condition in the extant taxa used to derive the regression formulas.

In the present contribution, we further test a recently proposed volumetric method based on hyper-realistic *in vivo* 3D reconstructions, using the anancine gomphotheriid *Anancus arvernensis* (Croizet and Jobert, 1828), and compare the results with the BM obtained from the classical regression formulas. Indeed, *Anancus* limb bones are thought to be robust and massive (Ferretti and Croitor, 2001), suggesting that regression formulas based on stylopods may overestimate the weight.

Anancus arvernensis (Croizet and Jobert, 1828) belongs to the anancine gomphotheres, a clade of Elephantoidea that originated in Eurasia, probably derived from *Tetralophodon*, and it is currently the only widely accepted species of this genus for western Europe. Anancines, which are found only in Europe, Africa and Asia (Hautier et al., 2009), are distinguished among Elephantoidea by having an anancoid condition in their dental morphology, as well as an apomorphic character characterised by an alternation of pretrite and posttrite half-loph(id)s (Tassy, 1986; Hautier et al., 2009).

The genus *Anancus*, with a Late Miocene–Early Pleistocene distribution (Hautier et al., 2009), probably originated in Asia between 9.0 and 8.5 Ma, entering Europe around 7.2 Ma (the second half of the Turolian) (Konidaris and Roussiakis, 2018). The taxon is characterised by a high and short skull with an elevated dome. The mandible is short without tusks, the upper tusks are straight without enamel, the premolars are absent, the intermediate molars are tetralophodont, and the upper third molars have five or six lophs (Tassy, 1986; Garrido and Arribas, 2014; Konidaris and Roussiakis, 2018). The enamel folding ranges from coarse to fine, and the molar crown is simple or complex, with clear alternation of the pretrite and posttrite half-lophs (anancoidy), particularly in m3 (Tassy, 1986; Garrido and Arriba, 2014 and references therein).

Traditionally, bunodont molars have been associated with a diet that consists of soft vegetables, such as fruit, leaves and twigs. Rivals et al. (2015) examined the tooth microwear of the three proboscidean taxa *Mammuthus rumanus*, *M. meridionalis* and *A. arvernensis* that co-occurred in Early Pleistocene localities of Europe (i.e. Red Crag, Norwich Crag, Chilhac and Eastern Scheldt). The detected microwear pattern indicates a possible niche partitioning reducing direct competition, with the *Mammuthus* diet probably including more grit (an indication of more open to semi-open habitats) while *Anancus* was feeding essentially on fruit, bark, twigs and seeds (Rivals et al., 2015). Autopod structure in *Anancus* has been interpreted as well-suited for locomotion in soft substrates, thus identifying moist woodlands as typical palaeoenvironments for the taxon (Braber et al., 1999; Mol et al., 1999; Rivals et al., 2015).

Anancus arvernensis was widespread in the Pliocene and Early Pleistocene European large mammal assemblages. All the forms from Europe can be very likely referred to the single taxon *A. arvernensis* (Schlesinger, 1917; Metz-Muller, 1995; Garrido and Arribas, 2014), with a possible trend towards crown simplification, molar shortening, and an increase in hypsodonty (Metz-Muller, 1995). Garrido and Arribas (2014) recognise five valid subspecies within the genus.

In the Italian peninsula, *Anancus* is recorded from the lower Villafranchian (Upper Pliocene, Piacenzian) to the middle Villafranchian (Upper Pleistocene, Gelasian partim) European Land Mammal Ages (Triversa to Coste San Giacomo Faunal Units in the biochronological scheme proposed by Gliozzi et al. (1997) for the Italian mammalian assemblages). In particular, in the Coste San Giacomo site the possible coexistence of *A. arvernensis* with *M. meridionalis* has been recorded (Bellucci et al., 2012; Bellucci et al., 2014).

The BM estimate of *Anancus* in the present contribution was conducted starting from two fairly complete mounted skeletons, housed and exhibited, respectively, at the Museum of Geology and Palaeontology of the University of Florence (Italy) (labelled IGF 319, 'Val' herein) (Figure 1), and the Museum of Geology and Palaeontology 'Giuseppe Capellini' of the University of Bologna (Italy) (labelled MGGC 8441, 'VA' herein) (Figure 2). Information about the original excavation, recovery, assembly and initial studies of the two specimens is provided in Appendix 1. The aim of the work is to provide a BM for *A. arvernensis* as close as possible to the natural condition, and a first *in vivo* hyper-realistic 3D reconstruction for the mastodon, as well as to provide further discussion points on the performance of different approaches to BM estimation in extinct terrestrial tetrapods.

MATERIAL AND METHODS

Both the application of the classical regression formulas and the volumetric estimation using the 3D method were carried out based on two mounted specimens of *A. arvernensis*: the specimen from Montecarlo exhibited at the Museum of Geology and Palaeontology of the University of Florence (Italy) (specimen IGF 319) and the skeleton from Ca' dei Boschi exhibited at the Geological and Paleontological Museum 'Giovanni Capellini' of Bologna (Italy) (specimen MGGC 8441). We measured the *Anancus* long-bone elements of the two specimens directly with digital callipers for measurements less than 300 mm and dial callipers for measurements longer 300 mm; a flexible measuring tape was used for bone circumferences. Only bones with optimal 3D preservation and not subjected to distortion or compression during diagenesis were measured and considered for the present

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Figure 1. The mounted skeleton of *Anancus arvernensis* exhibited at the Museum of Geology and Palaeontology of the University of Florence (Italy) ('Val', labelled IGF 319). Above the skeleton the DJI Mavic Air 2 drone is visible taking photos for the 3D model.

Figure 2. The mounted skeleton of *Anancus arvernensis* exhibited at the Museum of Geology and Palaeontology 'Giuseppe Capellini' (Bologna University) (VA, labelled MGGC 8441).

study. In any case, individual bones or portions of bones that led to results that were too implausible were progressively discarded in the estimation of the final BM (see below). Measurements of available long bones and considered appendicular elements are reported in Tables 1, 4 and 5. The procedure for 3D reconstruction of skeletons and digital sculpting of soft tissue is described below.

Body mass and shoulder height estimate: regression equations

Among the diverse predictive formulas recommended by the authors for estimating the proboscidean BM, the regression equations proposed by Roth (1990) cannot be confidently used to predict the BM of large continental species, including *A. arvernensis*, being specifically proposed for dwarf elephants (see Roth, 1990, Table 9.1, p. 158). Therefore, we have chosen to calculate the BM of *A. arvernensis* specimens from Ca' dei Boschi (VA) and Montecarlo (Val) using the widely employed Christiansen's (2004) regression equations, based on the specific linear dimensions of the left and right long bones of the forelimb and hindlimb stylopodia and zeugopodia.

All measurements were taken from both sides of the specimen, when possible, and were subsequently averaged. The measurements herein used to estimate the BM of the *A. arvernensis* specimens from Ca' dei Boschi (VA) and Montecarlo (Val) are those used by Christiansen (2004) for the database on which the author based his regression equations.

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Table 1. Body mass (BM) estimates of *Anancus arvernensis* specimens from Villafranca d'Asti (Capellini Palaeontological Museum, Bologna) and Valdarno (Geological and Palaeontological Museum, Florence) calculated using Christiansen's (2004) formula: log (BM) = a + b(logX) X=bone variables. Abbreviations as in Appendix.

Anancus arvernensis – body mass estimates (kg)

						Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)				
						Bone measurement (mm)		log(BM)		Estimated body mass (kg)
Variable	a ± 95% CI	b ± 95% CI	r	%SEE	%PE	sx	dx	sx	dx	sx
					Humerus					
Humerus maximum length	-4145	2635	0.99	11.52	6.74	875	862	3.60719121971379	3.59006164544812	4047.5406
Humerus least circumference of diaphysis	-1598	2062	0.995	7.78	5.54	388	388	3.74017101817526	3.74017101817526	5497.5731
Humerus diaphysial diameter in the anteroposterior plane	-0.503	2009	0.997	5.97	3.62	145	144	3.83918831649006	3.83315024661936	6905.3916
Humerus diaphysial diameter in the lateromedial plane	-0.66	2124	0.989	12.21	8.56	98	94	3.6936418477086	3.53092356104576	3709.9169
Humerus width of distal articular surface	-5.29	3872	0.96	24.33	16.72	188	214	3.51553919234897	3.73336213040807	3277.4735
Humerus medial condyle length	-2554	2943	0.881	43.15	28.34	185	160	4.11828639669007	3.93272510895639	**13 130.6551**
Humerus medial condyle width	-3202	3409	0.944	29.09	18.51	102	107	3.64531798553638	3.71616929812888	4418.9387
Humerus lateral condyle length	-2294	2867	0.904	39.34	25.43	140	133	3.85894907828951	3.79508265465263	7226.8506
Humerus lateral condyle width	-3784	3775	0.752	66.58	39.61	90	83	3.59326547313345	3.46051979871968	3919.81412
Average BM humerus										**6010.82**
Average BM humerus*										**4875.43**
					Radius					
Radius maximum length	-3838	2634	0.992	10.11	6.64	680	575	3.62282847606823	3.43096510291249	4195.9323
Radius least circumference of diaphysis	-0.754	2001	0.972	20.04	12.3	182	194	3.76840284735813	3.82389126159038	5866.8211
Radius diaphysial diameter in the anteroposterior plane	-0.43	1834	0.958	24.91	15.31	76	71	3.01941212824297	2.96520781155078	**1045.7120**
Radius diaphysial diameter in the lateromedial plane	-0.351	1969	0.96	26.01	16.3	44	41	2.8849583200013	2.82457141388116	**767.28784**
Average radius										**2968.93**
Average radius*										**5031.37**
					Ulna					
Ulna maximum length	-4135	2674	0.995	8.41	5.34	798	760	3.62495573147185	3.56829554575884	4216.5352
Ulna least circumference of diaphysis	-1349	2022	0.997	5.78	4.42	315	312	3.70258393976257	3.69418058910529	5041.7805
Ulna diaphysial diameter in the anteroposterior plane	-0.872	2304	0.974	19.16	11.79	114	105	3.86710877747923	3.78482014505714	7363.91517
Ulna diaphysial diameter in the lateromedial plane	-0.185	1743	0.992	10.48	7.88	85	70	3.17797718752001	3.03100588374485	**1506.5279**
Average ulna										**4532.18**
Average ulna*										**5540.74**
					Femur					
Femur maximum length	-5568	3036	0.985	14.54	6.15	980	*995*	3.51336236580241	3.53339087314402	3261.0868
Femur least circumference of diaphysis	-1606	2073	0.976	18.46	11.52	363	363	3.70068643369986	3.70068643369986	5019.8002
Femur diaphysial diameter in the anteroposterior plane	-0.912	2315	0.98	16.64	11.4	130	133	3.98177886059033	4.0047165488388	**9589.1223**
Femur diaphysial diameter in the	-0.342	1904	0.966	22.23	14.42	103	103	3.49044207583865	3.49044207583865	3093.4426

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Table 1. (*Continued*)

Anancus arvernensis – body mass estimates (kg)

						Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)				
						Bone measurement (mm)		log(BM)		Estimated body mass (kg)
Variable	a ± 95% CI	b ± 95% CI	r	%SEE	%PE	sx	dx	sx	dx	sx
lateromedial plane										
Humerus width of distal articular surface	-4347	3502	0.928	33.49	21.71	214	*193*	3.81410903426887	3.65702169614522	6517.9201
Femur medial condyle length	-0.819	2156	0.862	23.42	15.35	220	*199*	4.23126329985268	4.13732723273933	**17 031.9078**
Femur medial condyle width	-1.55	2619	0.95	27.39	17.71	95	99	3.62965812225149	3.67656857465098	4262.4384
Femur lateral condyle length	-4.97	4345	0.833	53.49	30.98	207	221	5.09289115101031	5.21638442916181	**21 618.8439**
Femur lateral condyle width	-1514	2695	0.987	13.21	9.91	76	65	3.55479263119673	3.37180149615249	3587.5059
Average femur										**8840.12**
Average femur*										**4290.36**
					Tibia					
Tibia maximum length	-3064	2378	0.988	12.47	6.93	645	660	3.61713300140267	3.64087547871856	4141.2648
Tibia least circumference of diaphysis	-2724	2647	0.991	10.72	6.57	290	297	3.79396750043854	3.82138632134266	6222.5371
Tibia diaphysial diameter in the anteroposterior plane	-1044	1395	0.973	19.46	13.71	*98*	*100*	1.73376037559103	1.746	**54.17019**
Tibia diaphysial diameter in the lateromedial plane	-0.95	1391	0.97	20.82	14.12	*87*	*94*	1.7478712803925	1.79462084435718	**55.9591**
Average tibia										**55.9591**
Average tibia*										**5181.9009**
					Fibula					
Fibula maximum length	-3086	2422	0.975	18.68	11.4	?	?			
Fibula least circumference of diaphysis	-0.483	2097	0.993	9.57	6.24	138	124	4.0493703	3.9068598	**11 203.9277614662**
Fibula diaphysial diameter in the anteroposterior plane	-1695	1263	0.959	24.62	17.31	*54*	*43*	0.493013318656409	0.368070659397018	**3.11181176663127**
Fibula diaphysial diameter in the lateromedial plane	-2.02	1215	0.932	32.38	19.97	*27*	*32*	0.28083027	0.523507347472116	**0.523729423362958**
Average fibula										**0.523729423362958**

Anancus arvernensis – body mass estimates (kg)

	Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)		Upper Valdarno, composite skeleton (Geological and Palaeontological Museum, Florence)						
	Estimated body mass (kg)		Bone measurement (mm)		log(BM)		Estimated body mass (kg)		
Variable	dx	sx+dx/2	sx	dx	sx	dx	sx	dx	sx+dx/2
	Humerus					**Humerus**			
Humerus maximum length	3891.0037	3969.2721	875	-	2.94200805302231	-	4048	-	4048
Humerus least circumference of	5497.5731	5497.5731	405	-	2.60745502321467	-	6006	-	6006

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Table 1. (*Continued*)

Anancus arvernensis – body mass estimates (kg)

	Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)		Upper Valdarno, composite skeleton (Geological and Palaeontological Museum, Florence)						
	Estimated body mass (kg)		Bone measurement (mm)		log(BM)		Estimated body mass (kg)		
Variable	dx	sx+dx/2	sx	dx	sx	dx	sx	dx	sx+dx/2
diaphysis									
Humerus diaphysial diameter in the anteroposterior plane	6810.0491	6857.7204	151	-	2.17897694729317	-	7491	-	7491
Humerus diaphysial diameter in the lateromedial plane	3395.6550	3552.7859	97	-	1.98677173426624	-	3630	-	3630
Humerus width of distal articular surface	5412.0541	4344.7638	226	-	2.3541084391474	-	6685	-	6685
Humerus medial condyle length	**8564.9554**	**10 847.8053**	166	-	2.22010808804005	-	**9545**	**-**	**9545**
Humerus medial condyle width	5201.9874	4810.46310	112	-	2.04921802267018	-	6078	-	6078
Humerus lateral condyle length	6238.53555	6732.6930	142	-	2.15228834438306	-	7527	-	7527
Humerus lateral condyle width	2887.48541	3403.6497	101	-	2.0043	-	6058	-	6058
Average BM humerus	**5501.03**	**5557.41**					**6340.87**		**6340.86**
Average BM humerus*	**4916.79**	**4896.11**					**5940.34**		**5940.34**
	Radius					**Radius**			
Radius maximum length	2697.5226	3446.72750	698	-	2.84385542262316	-	4495	-	4495
Radius least circumference of diaphysis	6666.3983	6266.6097	190	-	2.7875360095283	-	6394		6394
Radius diaphysial diameter in the anteroposterior plane	**923.01298**	**984.3625**	65	-	1.81291335664286	-	785		785
Radius diaphysial diameter in the lateromedial plane	**667.6846**	**717.4862**	51	-	1.70757017609794	-	1026		1026
Average radius	**2738.65**	**2853.79**					**3175.05**		**3175.05**
Average radius*	**4681.96**	**4856.66**					**5444.52**		**5444.52**
	Ulna					**Ulna**			
Ulna maximum length	3700.7994	3958.6673	780	760	2.89209460269048	2.88081359228079		3701	3834
Ulna least circumference of diaphysis	4945.1627	4993.4716	354	307	2.54900326202579	2.48713837547719		4786	5585
Ulna diaphysial diameter in the anteroposterior plane	6092.8452	3986.5998	102	108	2.00860017176192	2.3342375548695		6501	6100
Ulna diaphysial diameter in the lateromedial plane	**1074.0039**	**1290.2659**	89	98	1.94939000664491	1.99122607569249		**1931**	**1781**
Average ulna	**3953.21**	**424.69**					**4420.5822**	**4229.7797**	**4325.1810**
Average ulna*	**4912.94**	**5226.66**					**5350.03**	**4496.00**	**4448.00**
	Femur								
Femur maximum length	3415.0012	3338.04407							
Femur least circumference of diaphysis	5019.8002	5019.8002							
Femur diaphysial diameter in the	**10 109.1944**	**9849.1583**							

(*Continued*)

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Table 1. (*Continued*)

Anancus arvernensis – body mass estimates (kg)									
	Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)		Upper Valdarno, composite skeleton (Geological and Palaeontological Museum, Florence)						
	Estimated body mass (kg)		Bone measurement (mm)		log(BM)		Estimated body mass (kg)		
Variable	dx	sx+dx/2	sx	dx	sx	dx	sx	dx	sx+dx/2
anteroposterior plane									
Femur diaphysial diameter in the lateromedial plane	3093.4426	3093.4426							
Humerus width of distal articular surface	4539.6429	5528.7815							
Femur medial condyle length	**13 719.1508**	**15 375.5293**							
Femur medial condyle width	4748.6326	4505.5355							
Femur lateral condyle length	**26 020.8287**	**23 819.8363**							
Femur lateral condyle width	2353.9731	2970.7395							
Average femur	**8700.58**	**8166.76**							
Average femur*	**3861.75**	**4076.06**							
	Tibia								
Tibia maximum length	4373.9667	4257.6157							
Tibia least circumference of diaphysis	6628.0583	6425.2977							
Tibia diaphysial diameter in the anteroposterior plane	**55.7185**	**54.9443**							
Tibia diaphysial diameter in the lateromedial plane	**62.3190**	**59.139**							
Average tibia	**62.310**	**59.1346**							
Average tibia*	**5501.0125**	**5341.4567**							
	Fibula								
Fibula maximum length									
Fibula least circumference of diaphysis	**8069.74478732**	**9636.8362743931**							
Fibula diaphysial diameter in the anteroposterior plane	**2.33383774510046**	**2.72282475586587**							
Fibula diaphysial diameter in the lateromedial plane	**3.33816152679896**	**1.93094547508096**							
Average fibula	**3.33816152679896**	**1.0956**							

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Table 2. Statistical summary and normality text results obtained for the data samples of *Anancus arvernensis* from Villafranca d'Asti (Capellini Palaeontological Museum, Bologna) and Valdarno (Geological and Palaeontological Museum, Florence).

Anancus arvernensis – Villafranca d'Asti				*A. arvernensis* – Villafranca d'Asti				*Anancus arvernensis* – Valdarno			
Summary statistics – BM (in t)				Summary statistics (forelimb) – BM (in t)				Summary Statistics – BM (in t)			
	Sample VA-A	Sample VA-B	Sample VA-C		Sample VA-D	Sample VA-E	Sample VA-F		Sample Val-A	Sample Val-B	Sample Val-C
N	31	20	7	N	17	12	6	N	17	13	6
Min	**0.05**	**2.97**	**3.45**	**Min**	**0.72**	**3.45**	**3.45**	**Min**	**0.79**	**3.63**	**3.83**
Max	**23.82**	**6.86**	**6.86**	**Max**	**10.85**	**6.86**	**6.86**	**Max**	**9.55**	**7.53**	**7.49**
Sum	172.35	96.31	35.16	Sum	78.4	61.16	28.73	Sum	87.47	74.47	32.39
Mean	**5.559677**	48155	**5022**	**Mean**	**4.611765**	**5.096667**	**4.788333**	**Mean**	**5.145294**	**5.728462**	**5.376253**
Std. error	0.8445118	0.2873898	0.4951177	Std. error	0.6090332	0.3724964	0.515942	Std. error	0.5827787	0.3606935	0.5886732
Variance	22.1092	1651858	1175	Variance	6.305665	1.665042	1.597177	Variance	5.773726	1.691297	2.079217
Stand. dev	4.702042	1.285246	1309	Stand. dev	2.511108	1.290365	1.263795	Stand. dev	2.402858	1.300499	1.441949
Median	**4.51**	**4.66**	**4.99**	**Median**	**4.34**	**4.9**	**4.48**	**Median**	**6.01**	**6.06**	**5.25**
25 percentile	3.34	3.6525	3.96	25 percentile	3.425	3.9625	3.8325	25 percentile	3.8	4.27	4.03
75 percentile	6.73	6085	**6.43**	75 percentile	6.5	6615	5.84	75 percentile	6.54	6.54	6.6575
Skewness	**2272915**	**0.2704718**	**0.294434**	**Skewness**	**0.580899**	**0.221222**	0.8540474	**Skewness**	**-0.4117292**	**-0.377248**	**0.4213964**
Kurtosis	**7.107594**	**-1.195113**	**-1589**	**Kurtosis**	**1.196687**	**-1.616922**	**0.007847304**	**Kurtosis**	**-0.2158806**	**-003173**	**-1.65831**
Geom. mean	3.508438	4652614	4877375	Geom. mean	3.801024	4.947142	4.657813	Geom. mean	4.323501	5.5803	5.24137
Coeff. var	**84.57402**	**26589**	**25812**	**Coeff. var**	**54.45005**	**25.31783**	**26.3932**	**Coeff. var**	**46.70011**	**22.70241**	**26.711**
Normality test – BM (in t)				**Normality test (forelimb) – BM (in t)**				**Normality test – BM (in t)**			
	Sample VA-A	**Sample VA-B**	**Sample VA-C**		**Sample VA-D**	**Sample VA-E**	**Sample VA-F**		**Sample Val-A**	**Sample Val-B**	**Sample Val-C**
N	31	20	7	N	17	12	6	N	17	13	6
Shapiro-Wilk W	**0.79**	**0.9324**	**0.9269**	**Shapiro-Wilk W**	**0.9424**	**0.8965**	**0.9229**	**Shapiro-Wilk W**	**0.9424**	**0.9109**	**0.8957**
p(normal)	**0.0000338**	0.1716	0.5246	p(normal)	0.3472	0.1428	0.5267	p(normal)	0.348	0.1889	0.3489
Anderson-Darling A	**1.828**	**0.4078**	**0.2755**	**Anderson-Darling A**	**0.3556**	**0.4542**	**0.2937**	**Anderson-Darling A**	**0.4704**	**0.516**	**0.3398**
p(normal)	**0.0000865**	0.3159	0.5376	p(normal)	0.4165	0.2212	0.4758	p(normal)	0.2149	0.1544	0.3558
p(Monte Carlo)	**0.0001**	0.3306	0.6015	p(Monte Carlo)	0.4191	0.2287	0.5219	p(Monte Carlo)	0.2197	0.1593	0.3928
Lilliefors L	**0.2298**	**0.1211**	**0.2178**	**Lilliefors L**	**0.1382**	**0.1517**	**0.2414**	**Lilliefors L**	**0.1795**	**0.2011**	**0.2356**
p(normal)	**0.0001**	0.6096	0.3995	p(normal)	0.5155	0.6168	0.3355	p(normal)	0.1484	0.1554	0.3721
p(Monte Carlo)	**0.0005**	0.6094	0.4073	p(Monte Carlo)	0.5117	0.6198	0.3529	p(Monte Carlo)	0.1411	0.1606	0.3798
Jarque-Bera JB	**67.95**	**1,412**	**0.645**	**Jarque-Bera JB**	**0.9969**	**1168**	**0.5715**	**Jarque-Bera JB**	**0.5679**	**0.8779**	**0.6029**
p(normal)	**0.000000000000001753**	0.4935	0.7244	p(normal)	0.6075	0.5576	0.7514	p(normal)	0.7528	0.6447	0.7398
p(Monte Carlo)	**0.0001**	0.242	0.4545	p(Monte Carlo)	0.3877	0.2302	0.4977	p(Monte Carlo)	0.6729	0.4198	0.4625

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Table 3. Groups formed by including the BM estimates of Villafranca d'Asti and Valdarno *Anancus arvernensis* specimens, ordered according to the decreasing value of the regression coefficient (*r*), and the increasing values of the per cent standard error of the estimate (%SEE), and per cent prediction error (%PE) of the regression equations from which they were derived.

Anancus arvernensis (body mass in kg)						
Villafranca d'Asti (forelimb) (Capellini Palaeontological Museum, Bologna)						
	r		Body mass (kg) (Sample VA-D)		Body mass (kg) (Sample VA-E)	
Group	Value	Range	Average	Range	Average	Range
A	>0.9900	0.9900-0.9970	4287.67 (7)	1290-6858	4787.23 (6)	3447-6858
B	>0.9700	0.9700-0.9890	5515.93 (3)	3553-6728	5515.93 (3)	3553-6728
C	>0.9500	0.9580-0.9660	2015.54 (3)	717-4345	4344.67 (1)	4345
D	>0.9000	0.9040-0.9500	3703.50 (2)	4810-6733	3703.50 (2)	4810-6733
E	>0.7500	0.7520-0.8810	7125.73 (2)	3403-10848	3403.65 (1)	3403
	%SEE		Body mass (kg) (Sample VA-A)		Body mass (kg) (selected values)	
Group	Value	Range	Average	Range	Average	Range
A′	<11	5.78-10.72	4287.67 (7)	1290-6858	4787.23 (6)	3447-6858
B′	<20	11.52-19.46	4960.72 (2)	3553-6728	4960.72 (2)	3553-6728
C′	<30	20.04-29.09	3424.72 (5)	717-6267	5140.61 (3)	4345-6266
D′	<40	32.38-39.34	6372.69 (1)	6733	6372.69 (1)	6733
E′	<70	43.15-66.58	3403.65 (1)	3403-10848	3403.65 (1)	3403
	%PE		Body mass (kg) (Sample VA-A)		Body mass (kg) (selected values)	
Group	Value	Range	Average	Range	Average	Range
A″	<10	3.62-9.91	4195.81 (8)	1290-6858	4610.89 (7)	3446-6858
B″	<15	11.40-14.42	6497.49 (2)	6267-6728	6497.49 (2)	6267-6728
C″	<20	15.31-19.97	2714.27 (4)	717-4810	4577.61 (2)	4345-4810
D″	<30	21.71-28.34	7703.09 (2)	6733-10848	6762.69 (1)	6763
E″	<40	30.98-39.61	3403.65 (1)	3404	3403.65 (1)	3404
Villafranca d'Asti (forelimb and hindlimb) (Capellini Palaeontological Museum, Bologna)						
	r		Body mass (kg) (Sample VA-A)		Body mass (kg) (Sample VA-B)	
Group	Value	Range	Average	Range	Average	Range
A	>0.9900	0.9900-0.9970	5119.53 (9)	1290-9637	5021.24 (7)	3447-6858
B	>0.9700	0.9700-0.9890	4209.72 (10)	55-9849	4590.56 (7)	2971-5020
C	>0.9500	0.9580-0.9660	1828.55 (5)	3-4345	3719.10 (2)	3093-4345
D	>0.9000	0.9040-0.9500	4315.88 (5)	2-6733	5394.37 (4)	4506-6733
E	>0.7500	0.7520-0.8810	13 361.71 (4)	3403-23820	3403.65 (1)	3403.00
	%SEE		Body mass (kg) (Sample VA-A)		Body mass (kg) (Sample VA-B)	
Group	Value	Range	Average	Range	Average	Range
A′	<11	5.78-10.72	5119.53 (9)	1290-9637	5021.24 (7)	3447-6858
B′	<20	11.52-19.46	5102.36 (8)	2970-9849	4311.23 (7)	2970-6728
C′	<30	20.04-29.09	4016.01 (10)	3-15376	4604.16 (6)	3093-6266
D′	<40	32.38-39.34	4087.82 (3)	2-6733	4087.82 (2)	5529-6733
E′	<70	43.15-66.58	12 690.43 (3)	3403-23820	3403.65 (1)	3404
	%PE		Body mass (kg) (Sample VA-A)		Body mass (kg) (Sample VA-B)	
Group	Value	Range	Average	Range	Average	Range
A″	<10	3.62-9.91	4630.38 (13)	1290-9637	4478.90 (11)	2971-6858
B″	<15	11.40-14.42	4438.78 (7)	55-9849	5277.05 (4)	3093-6728
C″	<20	15.31-19.97	3842.84 (8)	2-4810	4553.58 (3)	4345-4810
D″	<30	21.71-28.34	7703.09 (3)	5529-10848	6130.74 (2)	5529-6733
E″	<40	30.98-39.61	13 611.74 (2)	3404-23820	3403.65 (1)	3404

(*Continued*)

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Table 3. (*Continued*)

Anancus arvernensis (body mass in kg)						
Upper Valdarno, composite skeleton (forelimb) (Geological and Palaeontological Museum, Florence)						
	r		Body mass (kg) (Sample Val-A)		Body mass (kg) (Sample Val-B)	
Group	Value	Range	Average	Range	Average	Range
A	>0.9900	0.9900-0.9970	4860.39 **(7)**	1781-7491	5243.10 (6)	3834-7491
B	>0.9700	0.9700-0.9890	4209.72 (3)	3630-6394	4209.72 (3)	3630-6394
C	>0.9500	0.9580-0.9660	2832.08 (3)	785-6685	6685.09 (1)	6685
D	>0.9000	0.9040-0.9500	6802.56 (2)	6078-7527	6802.56 (2)	6078-7527
E	>0.7500	0.7520-0.8810	7801.15 (2)	6058-9545	6057.77 (1)	6058
	%SEE		Body mass (kg) (Sample Val-A)		Body mass (kg) (Sample Val-B)	
Group	Value	Range	Average	Range	Average	Range
A′	<11	5.78-11.51	4860.39 (7)	1781-7491	5398.41(6)	3967-7491
B′	<20	11.51-19.46	4664.59 (2)	3630-5699	4664.59 (2)	3630-5699
C′	<30	20.04-29.09	4016.01 (5)	785-6685	6385.87 (3)	6078-6685
D′	<40	39.34	7526.80 (1)	7527	7526.80 (1)	7527
E′	<70	43.15-66.58	7801.15 (2)	6058-9545	6057.77 (1)	6058
	%PE		Body mass (kg) (Sample Val-A)		Body mass (kg) (Sample Val-B)	
Group	Value	Range	Average	Range	Average	Range
A″	<10	3.62-9.91	4608.75 (8)	1781-7491	5012.75 (7)	3967-7491
B″	<15	11.40-14.42	6247.26 (2)	6100-6394	6247.26 (2)	6100-6394
C″	<20	15.31-19.97	6381.71 (4)	785-6685	6381.71 (2)	6078-6685
D″	<30	21.71-28.34	8535.93 (2)	7527-9545	6130.74 (1)	5529-6733
E″	<40	30.980-39.61	6057.77 (1)	6058	6057.77 (1)	6058

We also applied the formulas proposed by Campione and Evans (2012) to estimate the weight of tetrapods, including pachyderms such as elephants and hippopotamuses. The regression equations are based on the circumferences and lengths of the femur and humerus, as well as the femur plus humerus last circumference combination, and were derived from a large dataset that included mammals and non-avian reptiles.

Regarding BM estimates in proboscideans based on shoulder height, since the forelimbs of *Anancus* are almost columnar (e.g. Ferretti and Croitor, 2001), we have calculated the stature of the VA and Val *A. arvernensis* mounted skeletons by applying the method proposed by Larramendi (2016) for the Elephantidae representatives, applying the formula proposed for adult proboscideans with roughly similar body proportions such as *Mastodon americanum*.

Statistical analysis

For the visual representation of variation in the studied data sets, we used explanatory data analysis diagrams known as box plots or whisker plots. Box plots visually show the distribution of numerical data and their skewness by displaying the data quartiles (or percentiles) and medians. A box plot is particularly useful for comparing distributions because the average value and the overall variation range are immediately apparent. In addition, the univariate analysis provides a number of basic descriptive statistics, including sample skewness and kurtosis. The related statistical summaries are effective and easy to read. We applied them to the BM estimates of the *A. arvernensis* specimens from VA and Val using four normality tests (Shapiro–Wilk, Anderson–Darling, Lilliefors and Jarque–Bera tests) to verify that each sample was taken from BM values with a normal distribution (null hypothesis). Among those applied, the Shapiro–Wilk and Anderson–Darling tests are considered to be the most exact, and the Lilliefors and Jarque–Bera tests are given as references. The normal distribution has to be rejected if the given *p*-value (normal) is <0.05. The data were generated in Past (the 'Evaluate Expression' module) using the normal and uniform random number generators (Hammer et al., 2001), with Monte Carlo replicates = 9999.

We applied statistical analysis to samples obtained by grouping the BM estimates, obtained for VA and Val specimens, into sets of data that differ from each other for the number and type of variables from which the BM estimates were derived. The samples are as follows: Samples VA-A and Val-A, which include all of the BM estimates obtained from the long bones of the fore and hindlimbs of VA and the long bones of the forelimb of the Val specimen, respectively; Samples VA-B and Val-B, which include the BM values selected after removing BM values that are too high or too low for animals with a size comparable to that of *Anancus* adult representatives; Samples VA-C and Val-C, which include only the variables used in the equations that have the highest regression coefficient (*r*), per cent standard error of the estimate (%SEE), and per cent prediction error (%PE) (best seven variables in Sample VA-C, six in Sample Val-C). Since the Val samples only include BM values derived from forelimb long-bone measurements, we also analysed Sample VA-D (all the variables), Sample VA-E (selected variables) and Sample VA-F (best six variables), which include the BM values obtained from the dimensions of the humerus, radius and ulna of the VA skeleton. This was done so that the BM estimates obtained for VA and Val specimens could be compared using analogous sets of data.

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Table 4. BM estimates of the *Anancus arvernensis* from Villafranca d'Asti (Capellini Palaeontological Museum, Bologna) and Valdarno (Geological and Palaeontological Museum, Florence) specimens obtained from their humerus and femur, and humerus circumferences, respectively, using the regression equations proposed by Campione and Evans (2012).

	Left	Right	log	log	a	b	log BM
Humerus least circumference of diaphysis	405		2.60745502321467		2.651	0.089	6.82336326654209
Humerus maximum length	875		2.94200805302231		2.802	1.716	6.52750656456852

Variable	Left	Right	log	log	a	b	log BM
H-circ. + F circ.	751	751	2.875639937	2.875639937	2.749	1.104	6.801134187
Femur circ.	363	363	2.559906625	2.559906625	2.818	0.417	6.796816869
Humerus circ.	388	388	2.588831726	2.588831726	2.651	0.089	6.773992905
Femur length	980	995	2.991226076	2.997823081	2.843	2.005	6.499055733
Humerus length	875	862	2.942008053	2.935507266	2.802	1.716	6.527506565

Anancus arvernensis – body mass estimates (kg)

Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)

	Bone measurement (mm)		log (BM)		Estimated body mass (kg)		
Variable	sx	dx	sx	dx	sx	dx	sx+dx/2
Femur least circumference of diaphysis	363	363	6.796816869	6.796816869	6263.496937	6263.496937	**6263.496937**
Humerus least circumference of diaphysis	388	388	6.773992905	6.773992905	5942.824492	5942.824492	**5942.824492**
Femur maximum length	980	995	6.499055733	6.517811019	3155.409532	3294.663151	**3225.0363415**
Humerus maximum length	875	862	6.527506565	6.509291359	3369.043082	3230.660776	**3299.851929**
Humerus circumference + femur circumference	751	751	6.801134187	6.801134187	6326.07282	6326.07282	**6326.07282**

Upper Valdarno, composite skeleton (Geological and Palaeontological Museum, Florence)

	Bone measurement (mm)		log (BM)		Estimated body mass (kg)		
Variable	sx	dx	sx	dx	sx	dx	sx+dx/2
Humerus least circumference of diaphysis	405	-	2.607455023	-	6658.29858141483	-	**6658.29858141483**
Humerus maximum length	875	-	2.942008053	-	3369.04308172534	-	**3369.04308172534**

Statistical analysis (to test the normal distribution of data, skewness and kurtosis) was performed using PAST 4.0 software (Hammer et al., 2001). The abbreviated codes herein used to indicate the provenance and current location of the studied *A. arvernensis* specimens and for long-bone measurements are reported in Appendix 2.

Volumetric body mass estimate

The volumetric estimates of the BM were obtained starting from two 3D digital models of the skeletons of *A. arvernensis* from Montecarlo and Ca' dei Boschi (Figures 3 and 4). Aerial photogrammetry was performed on the mounted skeletons of *Anancus* stored in the Natural History Museum of Florence and in the Geological and Palaeontological Museum 'Giovanni Capellini' of Bologna, by using the drone DJI Mavic Air 2. It is equipped with a 1/2″ CMOS Quad Bayer Sony IMX586 sensor camera, stabilised on a 3-axis gimbal, with resolution set at 12 MP. The infrared and the collision avoidance (Advanced Pilot Assistance Systems APAS 3.0) sensing systems ensured safer and more stable flight (Figure 1). The long-range transmission with the remote controller was guaranteed by OcuSync 2.0 technology (2.4 and 5.8 GHz), also permitting a display resolution of 1080p on the mobile device (i.e. smartphone) connected to the controller via the DJI Fly app.

The aerial surveys in the museums of Florence and Bologna lasted about 45 min, taking 370 and 396 pictures, respectively, of the two *Anancus* specimens. The skeleton stored in Florence was surveyed by acquiring images from different angles around the specimen, flying at different altitudes (i.e. 4 m, 3 m, 2 m, 1 m) (Figure 1).

The presence of a 2 m high protective glass barrier around the skeleton stored in Bologna (Figure 2) caused several difficulties for the aerial photogrammetric acquisition of the specimen. The survey started at an altitude of 2.5 m, and continued up to 4.5 m, with the aim of avoiding reflections on the glass, flying around and as closely as possible to the skeleton. However, the photogrammetric reconstruction based on the drone photos failed, not returning a satisfactory model. This is due to the presence of the non-removable historic glass structure protecting the mounted skeleton, which caused numerous mirrors of the specimen that generated spurious homologous points in the software. As a result, this has led to the repetition and duplication of skeletal portions, rendering the model unusable for the purposes of the present work. In this case we therefore used a scan of the skeleton obtained previously by DIAPReM (Centro Dipartimentale per lo Sviluppo di Procedure Automatiche Integrate per il Restauro dei Monumenti) (Figure 4), and kindly provided by Michela Contessi, curator of the Geological and Paleontological Museum 'Giovanni Capellini'. The model represents a point cloud not returning the original surface of the

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bones, but it is completely sufficient for the purpose of the present study. The point cloud was opened with the free software MeshLab, which enabled us to calculate the mesh and export the model as a 'Stanford ply' file.

Table 5. BM estimates of the *Anancus arvernensis* mounted skeletons from Villafranca d'Asti (Capellini Palaeontological Museum, Bologna) and Valdarno (Geological and Palaeontological Museum, Florence) obtained from their heights at the shoulder using the Larramendi (2015, 2016) formula. SH1 = skeletal height at the shoulder, corresponding to 95% of the sum of the bone maximal length; SH2 = physiological height at the shoulder, corresponding to 98% of the sum of the bone articular length.

Anancus arvernensis – body mass estimates (kg)				
Villafranca d'Asti (Capellini Palaeontological Museum, Bologna)				
Shoulder height (cm)				Body mass (kg)
Maximum length		Physiological length		Larramendi (2016)
Scapula	765	Scapula	765	
Humerus	875	Humerus	825	
Radius	698	Ulna	660	
Manus height	290	Manus height	290	
sSH 1 (cm)	**259**			**3529**
sSH 2 (cm)			**249**	**3289**
Average sSH				**3359**
Upper Valdarno (Geological and Palaeontological Museum, Florence)				
Shoulder height (cm)				Body mass (kg) Larramendi (2016)
Maximum length		Physiological length		
Scapula	830	Scapula	830	
Humerus	875	Humerus	860	
Radius	680	Ulna	610	
Manus height	285	Manus height	285	
SH 1 (cm)	**254**			**3356**
SH 2 (cm)			**253**	**3322**
Average sSH				**3339**

The two 3D models were then uploaded in ZBrush as a 'Stanford ply' file, software for sculpture and painting which also allows single bone elements to be isolated and anatomical corrections to be made to the skeleton models (see Romano et al., 2021a). In particular, before proceeding to the *in vivo* sculpturing of *Anancus*, some modifications were made to the Montecarlo specimen, taking as reference the skeletal graphs of the proboscideans proposed by Larramendi (2015). Specifically, the scapula was raised to the height of the neural spines, the feet were made more digitigrade by lifting the digits, and the vertebral curvature was straightened due to excessive downward bending in the area of the pelvic girdle (Figure 5). Next, the software ZBrush was used to digitally sculpt the soft tissue around the 3D models of the corrected skeletons in order to obtain an *in vivo* restoration of *A. arvernensis*. In previous studies on tetrapods for which no current analogues are available, three models, slim, average and fat, have been proposed (Romano and Manucci, 2019; Romano and Rubidge, 2019b; Romano et al., 2012b; Van den Brandt et al., 2023), suggesting three different body masses around the skeletons. In this way, it was possible to provide a range of soft tissue volumes and therefore a range of possible final BMs. However, in the present study, it was not necessary to reconstruct three different volumes, as the observable condition of muscle masses in present-day elephants can be used as a reference for estimating body masses. In particular, as in previous contributions (Romano et al., 2022b), the work by Morfeld et al. (2016) was used as a reference for fleshy masses in elephants in natural conditions (therefore avoiding obese or starving individuals) (Figures 6 and 7). Following a procedure recently applied in several clades of terrestrial tetrapods (Romano and Manucci, 2019; Romano and Rubidge, 2019b; Romano et al., 2021a, 2021b, 2022a) the sculpted models were uploaded to the software 3D Studio Max which allows the models to be scaled to real sizes and both the surface and the volume of the reconstructions to be calculated. The models were scaled by using as a reference the best preserved long-bone elements. To estimate the BM we then applied to the two obtained volumes a range of specific body density by using the values proposed by Larramendi (2016) for extinct proboscideans, ranging from 0.99 to 1.01 kg/1000 cm^3.

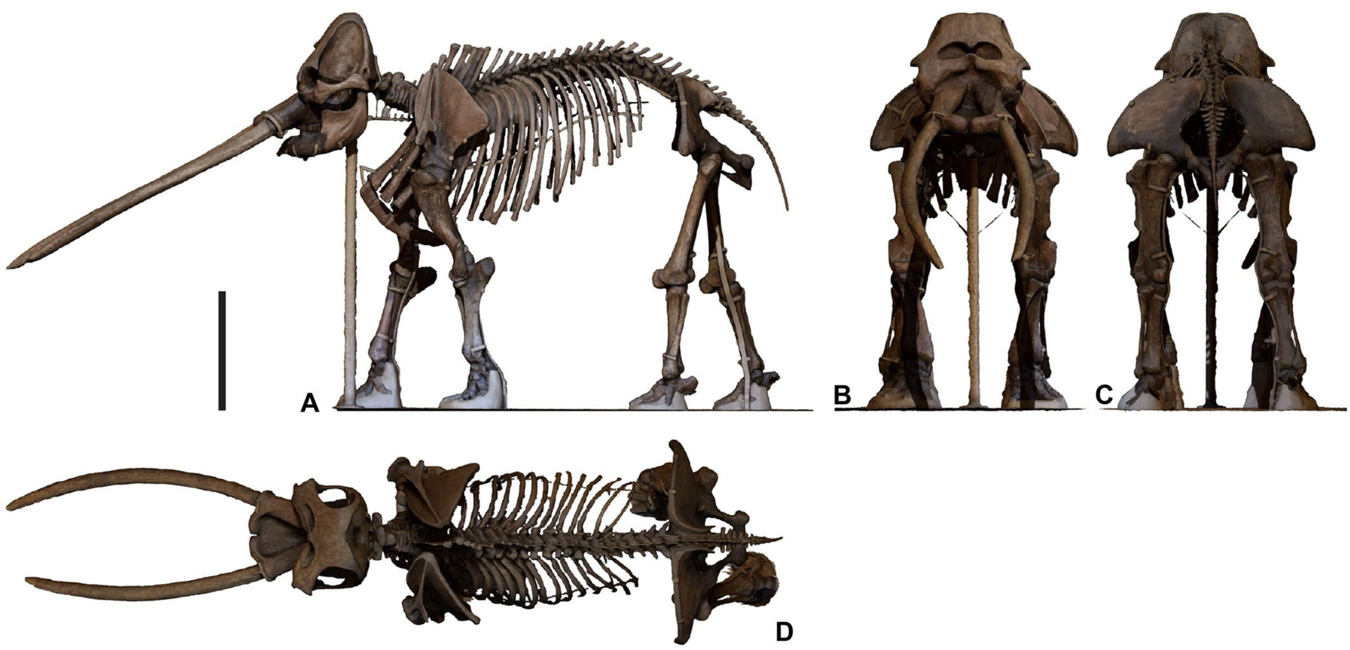

Figure 3. Photogrammetric 3D model of the original skeleton exhibited at the Museum of Geology and Palaeontology of the University of Florence (Italy). (A) lateral view, (B) front view, (C) posterior view, (D) dorsal view. Scale bar = 1 m. [Color figure can be viewed at wileyonlinelibrary.com]

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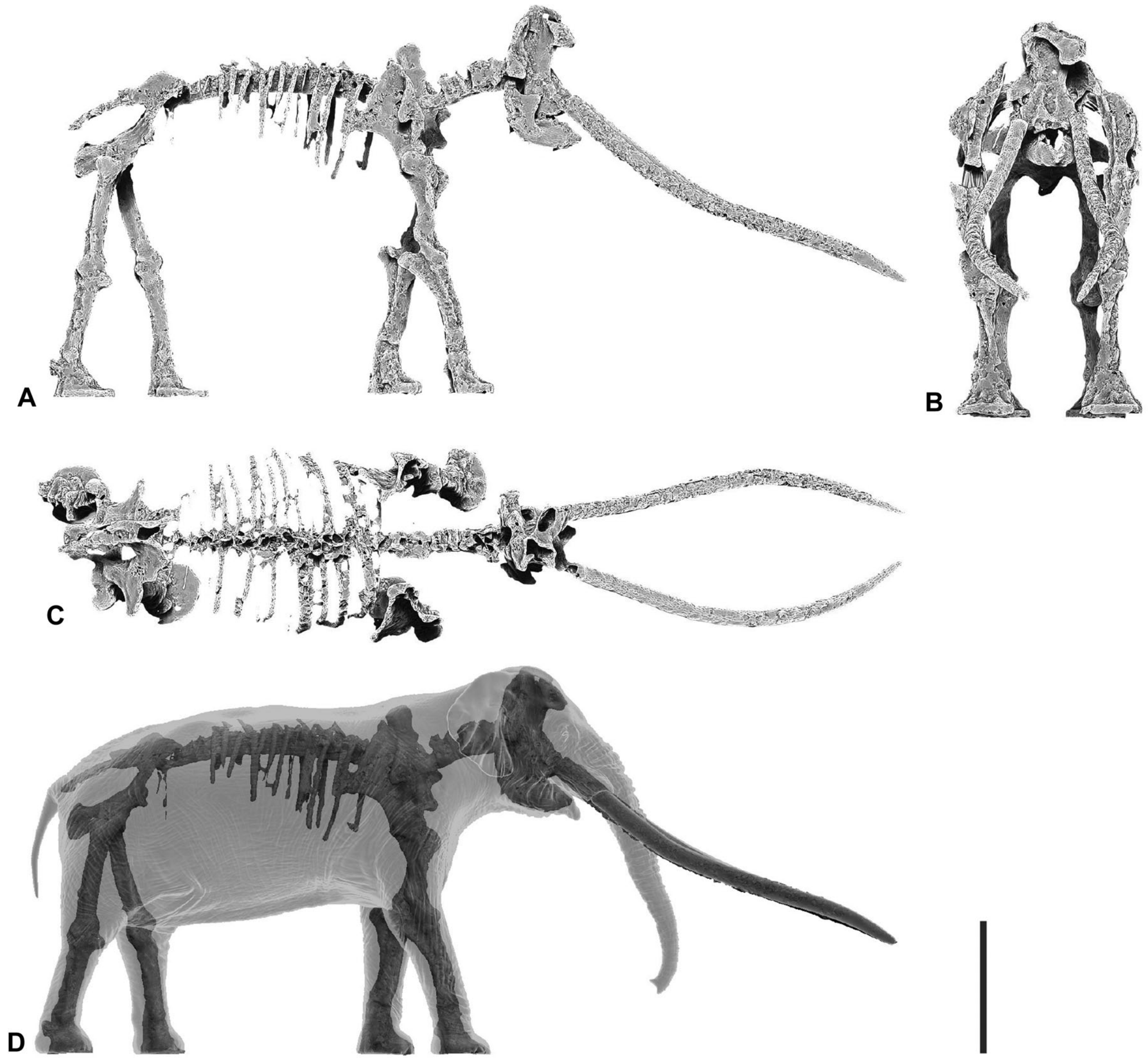

Figure 4. (A–C) Scan of the skeleton exhibited at the Museum of Geology and Palaeontology 'Giuseppe Capellini' (Bologna University) obtained previously by DIAPReM (Centro Dipartimentale per lo Sviluppo di Procedure Automatiche Integrate per il Restauro dei Monumenti). (D) Digital sculpture in transparency around the original skeleton. Scale bar = 1 m.

In several contributions on volumetric BM estimates, the density of water equal to 1 kg/1000 cm^3 has been considered as the most valid and conservative (e.g. Alexander, 1985, 1989; Gunga et al., 1995; Henderson, 1999; Hurlburt, 1999; Bargo et al., 2000; Hutchinson et al., 2007; Bates et al., 2009b; 2015; Larramendi, 2015; Larramendi et al., 2021). For all the above, we applied the three densities of 0.99, 1.00 and 1.01 kg/1000 cm^3 to the obtained volumes, in order to propose a possible range of BM as close as possible to the natural conditions.

RESULTS

Body mass and shoulder height estimates: regression equations

Anancus arvernensis from Ca' dei Boschi

The BM estimates, obtained for the VA *A. arvernensis* skeleton, using the available measurements among those suggested by Christiansen (2004) of the forelimb and hindlimb left and right long bones (Sample VA-A), shows a very large variation range. The BM values resulting from the regression of the measurements of the fibula diaphysis (Fi-diap.ap and Fi-diap.lm) are too low (2 kg and 3 kg) to be considered. However, even removing these variables, the range of BM values is still very large, ranging from 55 kg (T-diap.ap) to 23820 kg (F-lc) (Table 1), with an average BM estimate of about 5560 kg (Table 2). The coefficient of variation (84.57) is significantly larger than the maximum value (30.0) indicated for it to be considered acceptable (Table 2). In the normality test, all the *p*-values of the Anderson–Darling, Lilliefors and Jarque–Bera tests are significantly lower than 0.05, rejecting the null hypothesis of normally distributed data. The 'not normal' distribution of data is supported by the kurtosis and skewness indices, both reflecting a deviation from normality, the data distribution being asymmetrical and right long-tailed, with a major density of low values and a mean value greater than those of the median and mode (Table 2). Note that these BM values have been obtained by applying regression equations that have a per cent standard error of the estimate (%SEE) and a per cent prediction error (%PE) that, in the case of the fibula regression equations based on Fi.circ., Fi-diap.ap and FI-diap.lm variables, are moderately high (%SEE > 24.00, and %PE > 17.00), whereas the correlation coefficient is rather low ($r < 0.96$). In the case of the tibia, %SEE (>19) and %PE (>13) are not significantly high, and the correlation coefficient ($r > 0.97$) could be regarded as acceptable. Therefore, only the predicted BM values obtained from the fibula diaphysis deviate significantly from the regression line.

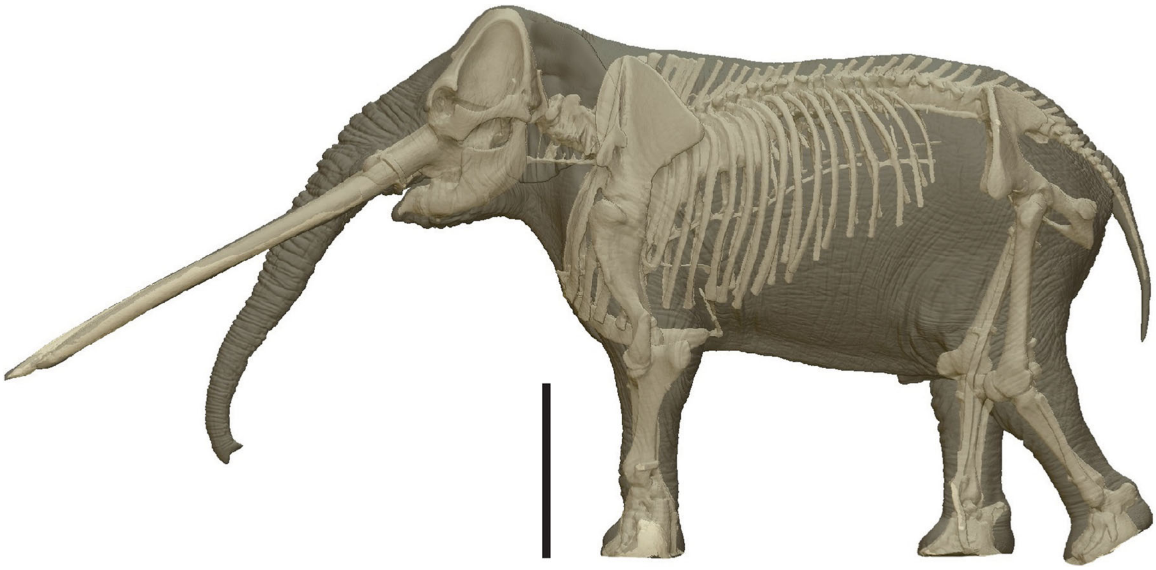

Figure 5. Digital sculpture in transparency around the modified skeleton of the specimen exhibited at the Museum of Geology and Palaeontology of the University of Florence. Scale bar = 1 m. [Color figure can be viewed at wileyonlinelibrary.com]

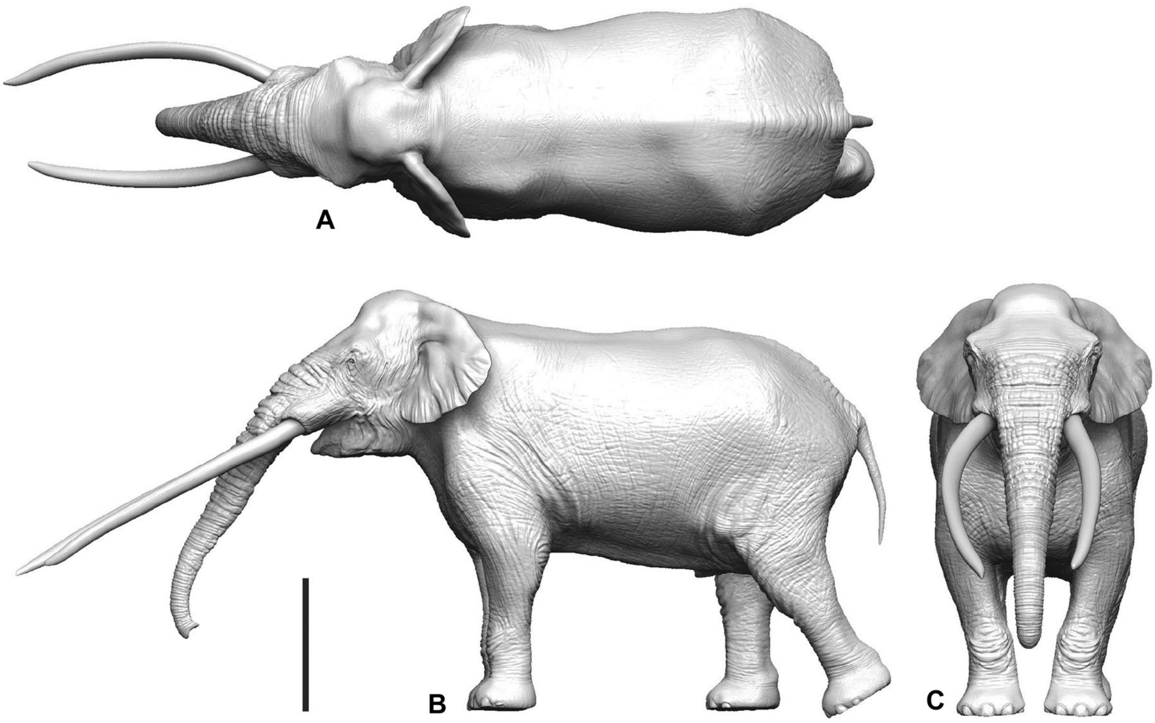

Figure 6. Solid model of *Anancus arvernensis* based on the corrected skeleton from the Museum of Geology and Palaeontology of the University of Florence in dorsal (A), lateral (B) and frontal (C) views. Scale bar = 1 m.

To obtain more compelling results, we conducted a new analysis after removing the highest (> 9000 kg) and lowest values (1500 kg) of BM estimates, which are objectively highly improbable for an animal of comparable size and structure to *Anancus* adult individuals. In the sample obtained by removing these BM values (Sample VA-B), the variation range reduces. The BM ranges from 2971 kg (F-lcw) to 6858 kg (H-diap.ap), with an average BM estimate of about 4816 kg (Table 1).

The coefficient of variation (26.69) is greater than the maximum value (20.0) to consider the mean value rather reliable but lower than the limit value (30) to consider it acceptable (Table 2). In the normality test, all the *p*-values of the Anderson–Darling, Lilliefors and Jarque–Bera tests are >0.05, indicating that the data are normally distributed. The values of the skewness and kurtosis indices are, respectively, slightly and moderately positive, and indicate a slight deviation from normality in the data distribution, which is right short-tailed (Table 1).

It is worth noting, however, that the predictive power of regression equations derived from some variables of Sample VA-B is still very low, and the corresponding BM estimates are not compelling, especially given that %SEE and %PE permit the predictive power of a regression equation to be evaluated better than *r*. Consequently, we have ordered and grouped the BM estimates of samples VA-A (including, in this case, even the BM values derived from fibula variables whose equations gave unrealistic BM estimates) and VA-B on the basis of the *r*,

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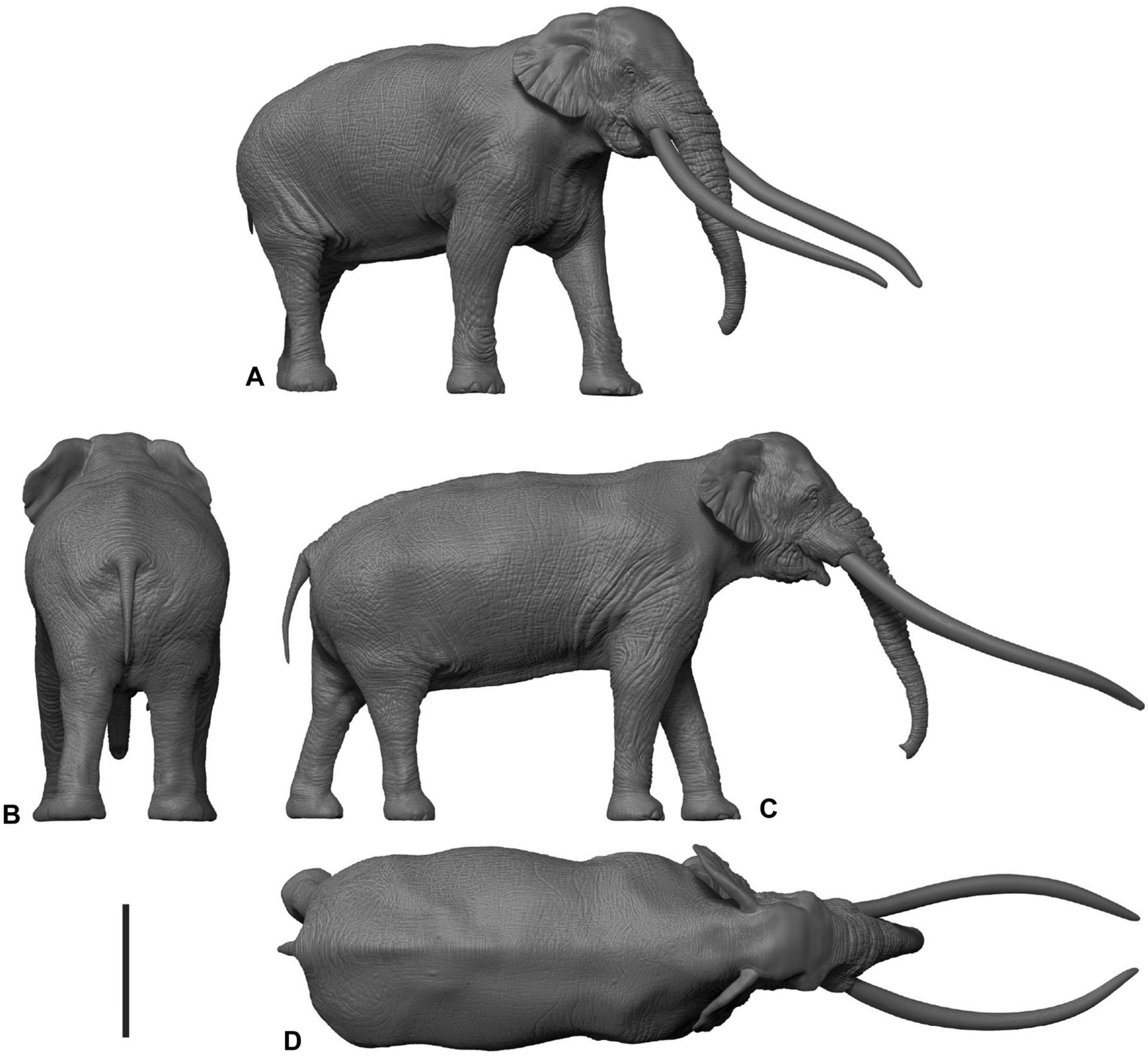

Figure 7. Solid model of *Anancus arvernensis* based on the skeleton from the Museum of Geology and Palaeontology 'Giuseppe Capellini' (Bologna University) in three-quarter (A), posterior (B), lateral (C) and dorsal (D) views. Scale bar = 1 m.

%SEE and %PE values of the equations from which they were generated. This was done in order to detect the group of variables that could provide the most reliable BM estimates (see Table 3). Nonetheless, there are a couple of BM estimates with rather high (9637 kg, Fi-circ.) and low (1290 kg, U-diap.lm.) values even in groups A, A′ and A″, which include the VA BM values estimated using the equations with the highest r (>0.9900) and the lowest %SEE (11) and %PE (10), respectively. Moreover, the variables and their numbers included in the three groups obtained for the regression coefficient and for %SEE and %PE change from one group to another, and the average BM estimates obtained for each group vary rather unpredictably. The average BM estimates included in each group also differ in the groups obtained for Sample VA-B, though to a lesser extent (Figure 8). Consequently, we operated a more restrictive selection, choosing the seven variables (Sample VA-C), which are present in all three groups A, A′ and A″ (i.e. H-length, H-circ., H-diap.ap, U-length, U-circ., R-length and T-circ.).

In the sample of these 'best seven' variables (Sample VA-C), the BM values ranges from 3447 kg (R-length) to 6858 kg (H-diap.ap). In the sample, high BM values related to the bone robustness prevail, as confirmed by the average BM value (5023 kg), and by the moderate asymmetrical distribution of data. Both kurtosis and skewness indices are moderately negative and the curve is left short-tailed.

Furthermore, because for the *A. arvernensis* specimens from Montopoli no measurements of the hindlimb bones are available, we limited the analysis to the BM values obtained for the VA forelimb for an easier comparison between the BM values obtained for VA and Val specimens. The VA-D sample still exhibits a wide range of variation (717–6858 kg) (Table 1). The coefficient of variation (54.45) is still significantly greater than the maximum value (30.0) for it to be considered acceptable (Table 2), but all of the p-values in the Anderson–Darling, Lilliefors and Jarque–Bera tests are greater than 0.05, and the null hypothesis of normally distributed data can be accepted, despite the fact that the kurtosis and skewness indices indicate a moderate deviation from normality, with the data distribution right-tailed with some major density of low BM values (Table 2).

In the sample obtained by removing the BM anomalous values (Sample VA-E), the BM ranges from 3404 kg to 6858 kg (Table 1). The average BM estimate of about 5096 kg could be regarded as still reliable because the coefficient of variation (25.21) is lower than the limit value (30) for it to be considered acceptable (Table 2). All the p-values of the normality tests are >0.05, indicating that the data are normally distributed, though the values of the skewness and kurtosis indices indicate a slight deviation from normality data distribution, and the curve is right short-tailed (Table 2).

In the sample with the 'best six' variables (Sample VA-F), the variation range of BM values is the same as that of Sample

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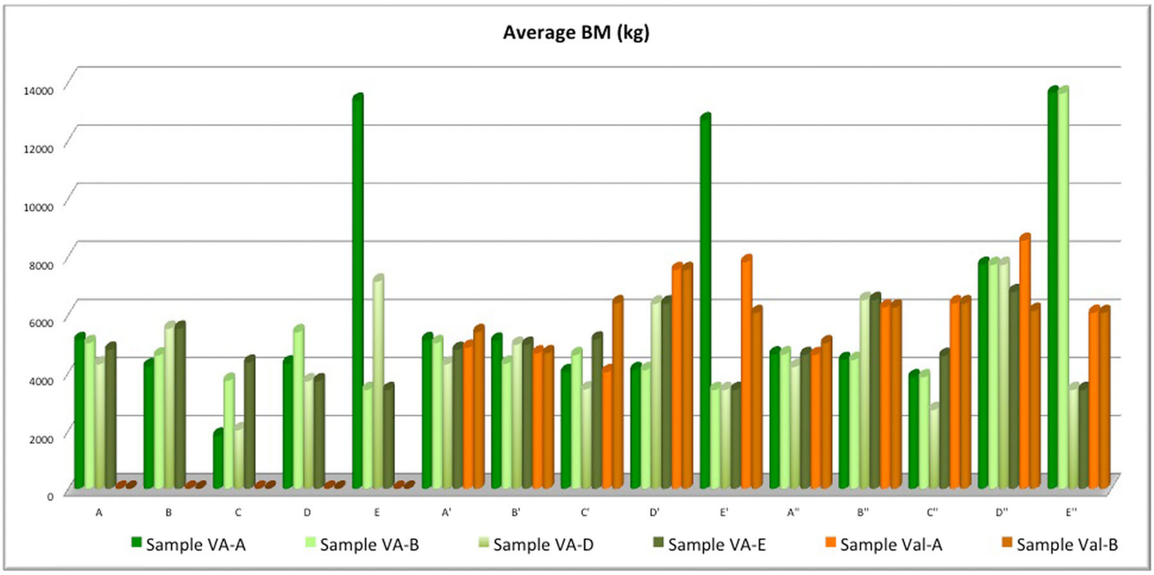

Figure 8. Comparison of the average body mass (BM) resulting from grouping the BM estimates obtained from forelimb and hindlimb long bone measurements (samples VA-A, VA-B and Va-C) and forelimb (VA-D), including the BM values derived from all variables, VA-D, including the BM values selected after removing BM values too high or too low for animals with a size comparable to that of *Anancus* adult representatives, and VA-E, including the six variables with either A, A′, and A″ = groups of BM values ordered according to the values of *r*, SSR% and PE% of the variables from which they were derived, respectively (see Table 3). [Color figure can be viewed at wileyonlinelibrary.com]

VA-E, but the coefficient of variation is slightly higher (26.39), whereas the BM average value is lower (4788 kg). The value of the kurtosis index, close to 0, suggests an almost symmetrical data distribution, though the curve is a little tailed on the right (Table 2).

In the box plot obtained by considering all BM estimates of the VA *A. arvernensis* specimen (Sample VA-A) (Figure 9), the BM estimate derived from the F-lcl variable (about 24 t) could be considered unrealistic, because its value falls further than three times the box height from the box (outer fence). The BM value derived from the F-mcl variable (15.4 t) is also too high, falling above the value which corresponds to the largest data point less than 1.5 times the box height (outlier), to which the BM value derived from the H-mcl variable (10.5 t) corresponds. This estimate of BM is the highest among all the other estimates of BM and corresponds to the upper inner fence, just above the BM obtained from F-diap.ap (about 1 t) and Fi-circ. (9637 kg). The other BM estimates based on humerus and femur measurements fall within the second and third quartile box or just above and below its border. The BM based on H-circ. (5498 kg) is the closest to the average BM estimated for Sample VA-A, which is definitely larger than the value of the median (4510 kg) (Tables 1 and 2). The lowest BM values (at the bottom of the first percentile, which includes all values below the box and above the lower inner fence), which have been derived from T-diap.am and T-diap ml (less than 1000 kg) variables, are improbable for an adult *A. arvernensis* individual, as they are BM estimates based on U.diap.lm, R-diap.lm and R-diap.ap, (less than 1500 kg), whereas the BM values obtained for the tibia diaphysial diameters (T-diap. ap, 55 kg, and T- diap.lm, 59 kg) are unrealistic even for an Anancidae calf (Table 1).

Outlines are absent in the box plot derived from the BM estimates included in Sample VA-B, and the BM variation ranges of quartiles are noticeably reduced, particularly in the first and fourth quartiles. Several BM scores obtained from the selected measurements fall within the second and third quartiles. The BM value derived from H-diap.ap (6858 kg), which matches the upper inner fence, and R-circ. (6267 kg) are the highest and lowest estimates, respectively, included in the fourth quartile, as the BM values derived from H-lcw (3404 kg) and F-lcw (2971 kg) are in the first quartile. The BM value derived from H-mcw (4810 kg) and F-mcw (4506 kg) are the BM estimates closer to the average value (4816 kg) and the median (4660 kg), which are lower and higher, respectively, than those of Sample VA-A, suggesting some prevalence of moderately high BM values (Figure 9, Tables 1 and 2).

The distribution of the BM value score in the box plot obtained for Sample VA-C is rather similar to that obtained for Sample VA-B, but the variation ranges of the first and fourth quartiles further decrease, whereas those of the second and third quartiles increase. The scores corresponding to the BM obtained by the best seven variables fall within these latter quartiles, except for H-diap.ap (6858 kg) and T-length (4258 kg), which match the values of the upper and lower inner fences, respectively. The BM average value (5023 kg) and the median value (4990 kg) are a little higher than in Sample VA-B (Figure 9, Tables 1 and 2).

As expected, the BM variation range reduces and no outliers are present, when only the BM values derived from the forelimb bone dimensions are analysed (Figure 10). In the Sample VA-D box plot, the range of the fourth quartile is the largest due to the differences among the BM values given by the H-mcl variable (1085 kg) with respect to those of H-diap.ap (6858 kg). H-lcl (6733 kg) and U-diap.ap (6728 kg), which are just a little higher than the BM values of the second and third quartiles. The lowest BM values are those derived from the radius diaphysial diameters (R-diap.lm, 717 kg, and R-diap.ap., 984 kg), which are appreciably lower than the minimum BM value included in the second quartile (H-lcw, 3404 kg). The BM estimate derived from H-dist.art (4345 kg) matches the median value. The quartile ranges, especially those of the first and fourth quartiles, further decrease when analysing Sample VA-E, where the BM estimates derived from H-diap.ap (6858 kg), R-length (3447 kg), U-circ (4993 kg) and H-mcw (4810 kg) are the highest, the lowest and the two values closest to the median, respectively. Finally, in the box plot obtained using the BM values derived from the best six variables (Sample VA-F), the ranges of the second and third quartiles further decrease, whereas that of the fourth quartile, in which the BM value derived from R-circ. (6267 kg) also falls, noticeably enlarges (Figure 10).

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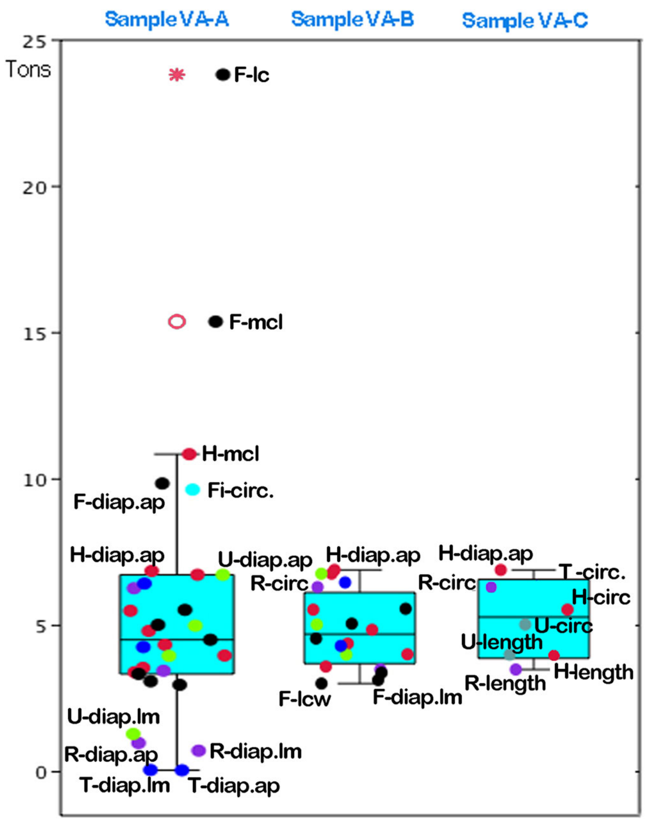

Figure 9. Box plot illustrating the variation range of body mass (BM) estimates obtained for the limb long-bone dimensions of the *Anancus arvernensis* skeleton on display at the Capellini Palaeontological Museum in Bologna. BM was calculated by averaging the BM obtained by measuring the left and right sides of the long bones. VA-A = the sample includes the BM estimates derived from all of the available measurements, among those suggested by Christiansen (2004); VA-B = the sample includes the BM values selected after removing BM values that were too high or too low for animals with a size comparable to that of *Anancus* adult representatives; VA-C = the sample includes the BM values derived from the variables used in all the equations that have the highest regression coefficient (*r*), per cent standard error of the estimate (%SEE), and per cent prediction error (% PE) (best seven variables). Star = BM values further than three times the box height from the box ('outer fences'); Circle = BM values higher than 1.5 times the box height (outliers). Abbreviations as in Appendix 2. [Color figure can be viewed at wileyonlinelibrary.com]

The application of Campione and Evans' (2012) formulas (Table 4), which are based on humerus and femur length and circumference, returned an average BM of 5011 kg, which roughly matches the average BM value (5023 kg) obtained using Christiansen's (2004) regression formulas derived from the best seven variables (Sample VA-C). The BM value obtained using the universal formula based on the combination of the femur and humerus circumferences, proposed by Campione and Evans (2012) as the best proxy for calculating the BM of extinct tetrapods, ranges from 4744 kg to 7908 kg, with an average BM of 6326 kg. The BM value ranges from 3558 kg to 9885 kg if the ±25% error proposed by the authors is added. Note that the BM values derived from the circumference (average BM value = 6103 kg) are definitely higher than those derived from length measurements (average BM value = 3262 kg), and those derived from the forelimb stylopodium (average BM value = 4621 kg) is slightly inferior to those obtained from the hindlimb ones (average BM value = 5014 kg). The BM estimates obtained from the same variables applying Christiansen's (2004) formulas (Table 1) are roughly consistent with those obtained using Campione and Evans' (2012) formulas, especially as regards the BM value derived from H-circ.

Finally, the BM values estimated using Larramendi's (2016) formulas based on the two adjusted shoulder heights of the VA mounted skeleton (sSH1 = 259 cm, corresponding to 95% of the sum of the bone maximal length, and physiological length; sSH2 = 249 cm, corresponding to 98% of the sum of the bones' articular length) are both lower (sSH1 BM = 3529 kg; sSH2 BM = 3289 kg) (Table 5) than those obtained using Christiansen's (2004) regression equations, but roughly consistent with the BM estimates derived from the forelimb bones and femur, using the same equations (Table 1). They are also consistent with the BM values derived from the humerus (3300 kg) and femur length (3225 kg), obtained by applying the formulas proposed by Campione and Evans (2012). Therefore, it might be supposed that the long-bone length underestimates the BM of *Anancus*, at least when the humerus and femur measurements are considered, and the hypothesis finds some support when comparing the average BM value derived from the length (3794 kg) to that returned by the circumference and diaphysial diameters (5107 kg) of VA long bones after removing the BM values > 9000 kg and <1500 kg (Table 1).

Anancus arvernensis from Montecarlo

We analysed the BM estimates obtained for the *A. arvernensis* skeleton from Montecarlo, following the same criteria adopted for the analysis of those obtained for the *A. arvernensis* specimen from Ca' dei Boschi.

The BM values of Sample Val-A show quite a large variation range (from 785 kg, R-diap.ap, to 9545 kg, H-mcl) (Table 1), with an average BM estimate of about 5145 kg (Table 2). The coefficient of variation (46.70) is definitely larger than the maximum value (30.0) for it to be considered acceptable (Table 2), but in the normality test all the *p*-values of the Anderson–Darling, Lilliefors and Jarque–Bera tests are >0.05, thus the data are normally distributed. The normal distribution of data is supported by the kurtosis and skewness indices, both with a value close to 0, though an unimportant negative deviation from normality is present due to the data distribution being a little asymmetrical, the curve being left short-tailed, and the median value being greater than that of the mode (Table 2).

We then ran a new analysis after removing the highest (>9000 kg) and the lowest values (<1500 kg) of BM estimates. In the obtained sample (Sample Val-B), the BM values range from 3630 kg (H-diap.lm) to 7491 kg (H-diap.ap), with an average BM value of about 5398 kg (Table 1). The coefficient of variation (22.70) is slightly larger than the maximum value (20.0) for the mean value to be considered reliable but <30, thus acceptable (Table 2). In the normality test, all the *p*-values are >0.05, indicating that the data are normally distributed. The values of the skewness and kurtosis indices are respectively slightly positive and moderately negative, hence there is a slight deviation from normality in the data distribution, which is left short-tailed (Table 1).

Since regression equations derived from some variables of Sample Val-B have a very low predictive power, we have attempted to detect the BM estimates originated by the variables with the highest predictive power by ordering and grouping the BM estimates for samples A and B, on the basis of the *r*, %SEE and %PE values of the equations from which they were generated (Table 3). The groups for *r*, %SEE and %PE differ in the type and number of variables included, and some unexpected BM values are present, such as the rather low BM estimate (1781 kg, U-diap.lm) in group A, which was derived from an equation with the highest *r* (>0.9900) and the lowest %SEE (11) and %PE (10) values. As a result, we chose the six variables (Sample Val-C) that are present in all three groups, A, A′ and A″, gathering the Val BM estimates, as well as

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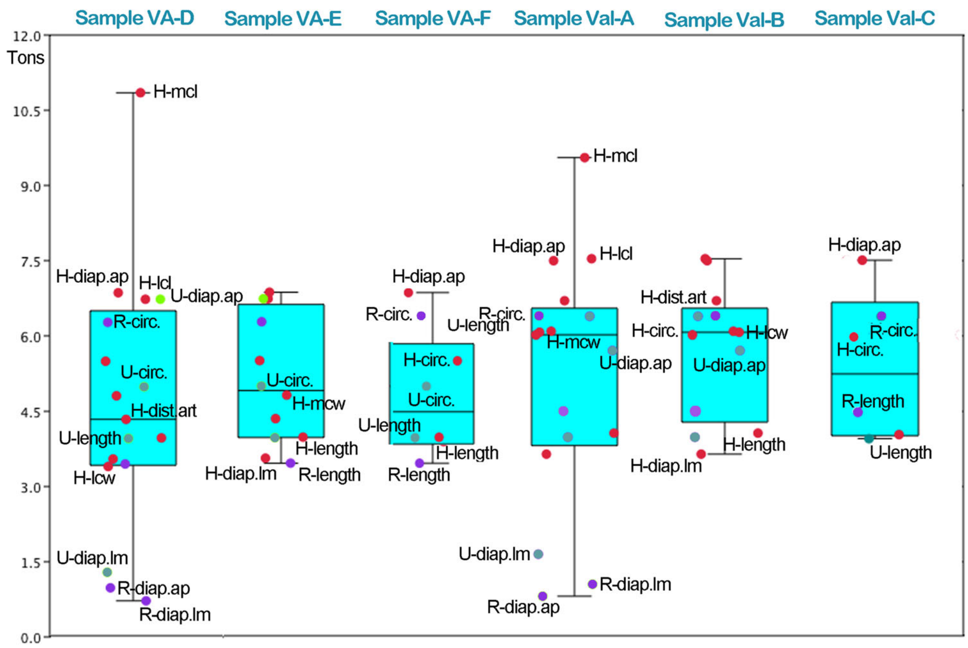

Figure 10. Comparison among the box plots that illustrate the variation range of the BM estimates obtained from the dimensions of the forelimb long bones of the two *Anancus arvernensis* specimens from Villafranca d'Asti (VA-D, VA-E and VA-F) (Capellini Palaeontological Museum, Bologna) and Valdarno (Val-A, Val-B and Val-C) (Geological and Palaeontological Museum, Florence). Symbols and abbreviations as in Figure 1. [Color figure can be viewed at wileyonlinelibrary.com]

Figure 11. *In vivo* restoration of *Anancus arvernensis* based on the mounted skeleton from 3D volumetric estimates built on the specimens from Ca' dei Boschi (VA). [Color figure can be viewed at wileyonlinelibrary.com]

in Sample VA-F (i.e. H-length, H-circ., H-diap.ap, U-length, U-circ. and R-length) (Table 3).

The BM estimates in Sample Val-C range from 3834 kg (U-length) to 7491 kg (H-diap.ap), with an average BM value of 5376 kg related to the bone robustness of the variables. The distribution of data is moderately asymmetrical, the skewness index being slightly positive and the kurtosis index moderately negative.

In the box plot obtained from analysing the BM estimates derived for Sample Val-A (Figure 10), the BM variation range is quite large but less than that obtained for Sample VA-A. Indeed, although H-mcl is still the variable that provides the highest BM value (9545 kg), the value is lower than that obtained for the VA specimen (10848 kg). Only some BM values obtained using humerus variables (H.cl, 7527 kg; H-diap.ap, 7491 kg; and H-dist.art, 6685 kg) fall within the fourth quartile, whereas the other three (H-mcw, 6078 kg; H-lcw, 6058; and H-circ., 6006 kg) are close to the median value (6010 kg). The lowest BM estimates are again those derived from the radius diaphysial diameters (R-diap.ap, 785 kg, and R-diap.lm, 1026 kg), as is the case for Sample VA-A.

In the box plot obtained for the Sample Val-B data, the quartile variation range decreases, especially that of the first and fourth. H-diap.ap is the variable that provides the highest BM estimate, whereas the lowest BM values were derived from the R-diap.ap. and R-diap.lm variables. The median value (6060 kg) is just slightly higher than that of Sample Val-A, underlining a prevalence in the Val-B sample of high BM values (Figure 10, Table 2). The median value is noticeably lower (5250 kg) in the box plot of Sample Val-C, where the variation range of the second and third quartiles slightly increases, probably because some humerus dimensions giving

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quite high BM values are not included among the best six variables. The first quartile only includes the lowest BM estimated in the sample (U-length, 4048 kg).

The application of formulas by Campione and Evans (2012) (Table 4) returned for the H-circ. variable a BM of 6658 kg, which is just slightly lower than that obtained applying Christiansen's (2004) regression formula (6006 kg) but definitely higher than that derived from H-length (3300 kg), which is in turn lower than that obtained with Christiansen's (2004) equation (4048 kg). The average BM value (5014 kg) is a little higher than that obtained for the VA specimen (4622 kg).

The BM values estimated by applying Larramendi's (2016) formulas based on the two adjusted shoulder heights of the Val mounted skeleton are almost the same (BM sSH1 = 3356 kg; BM sSH2 = 3322 kg), probably because of the proportionally short zeugopodium of the Val mounted skeleton, and, in turn, the low maximum length of the radius that affects sSH1 value (Table 5). As already observed with regard to the VA individual, the BM values derived from the shoulder height are lower than the BM average value obtained by applying the formulas proposed by Christiansen (2004) (Table 1), but consistent with the BM value derived from the humerus length using Campione and Evans' (2012) formula.

Volumetric body mass estimates

The 3D *in vivo* reconstruction sculpted on the base of the Val D'Arno specimen (Figure 6) when scaled on 3D Studio

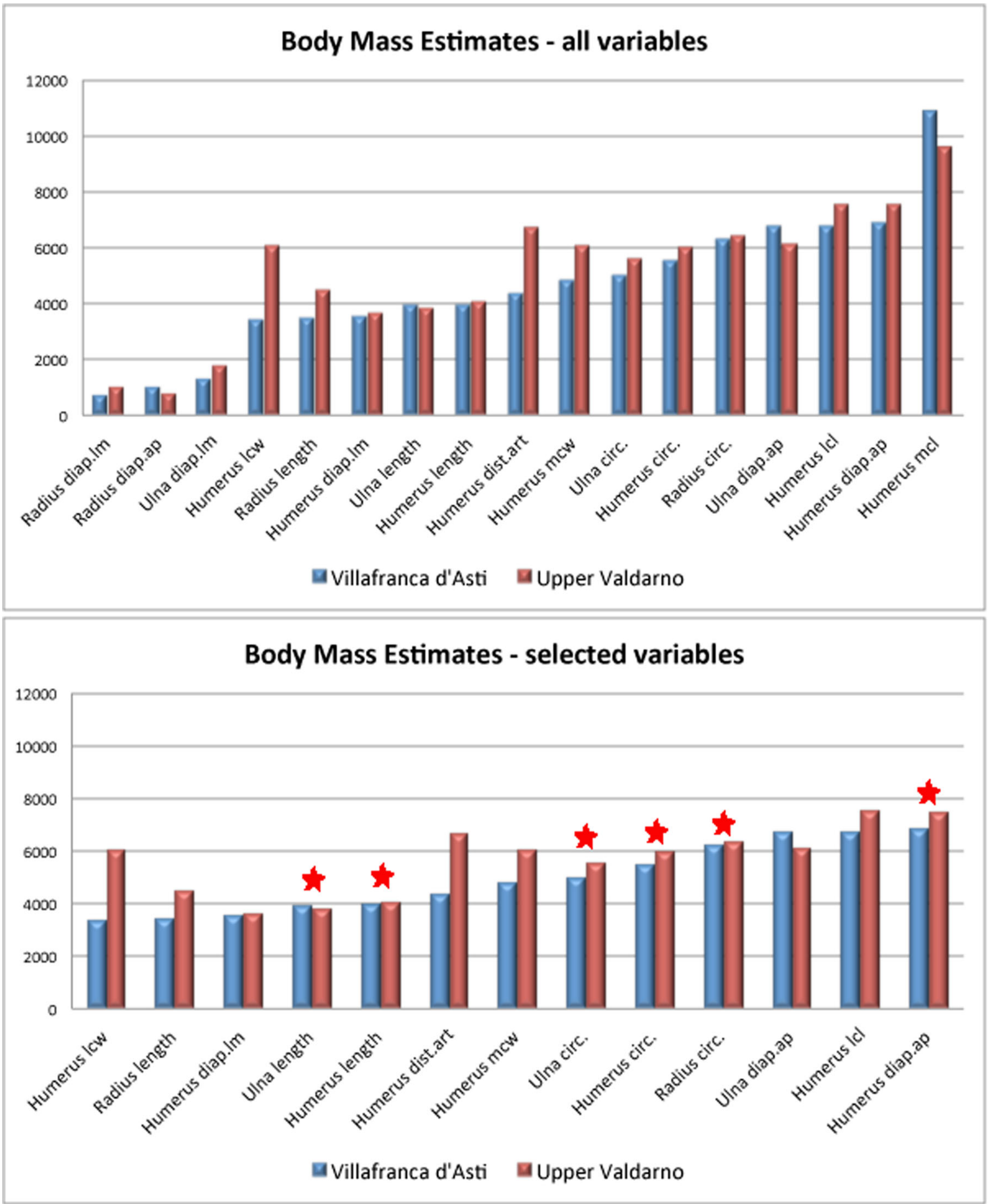

Figure 12. Histogram illustrating the differences in the average body mass (BM) values of each forelimb long bone of the *Anancus arvernensis* specimens from Villafranca d'Asti (Capellini Palaeontological Museum, Bologna) and Valdarno (Geological and Palaeontological Museum, Florence). The stars indicate the best six variables (samples VA-F, and Val-C).

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Max returned a total area of 27.5 m^2 and a volume equal to 5.21 m^3. By applying the three densities of 0.99, 1.00 and 1.01 kg/1000 cm^3 to the reconstructed volume, we obtained a BM respectively equal to 5160, 5210 and 5260 kg, with an average BM for the individual equal to 5210 kg.

The *in vivo* reconstruction of the specimen from Ca′ dei Boschi (Figure 7) once scaled is characterised by a surface area equal to 30.29 m^2 and a total volume of 6 m^3. The application of the three densities of 0.99, 1.00 and 1.01 kg/1000 cm^3 to the obtained volume in this case returned a BM respectively equal to 5940, 6000 and 6060 kg, with an average BM for the individual equal to 6000 kg.

In Figure 11 a possible *in vivo* reconstruction of *A. arvernensis* is proposed which, on the basis of the 3D volumetric estimates built on the specimen from Ca′ dei Boschi (VA) (distribution and volume of the soft parts digitally sculpted following the natural condition currently observed in living elephants; see Morfeld et al., 2016), could weigh between 5.2 and 6 t, a figure close to an extant adult male African elephant.

DISCUSSION

The results obtained confirm, from a methodological point of view, that microdrones are a useful and powerful tool for the reconstruction of 3D photogrammetric models of large skeletons mounted in museum exhibitions (see Romano et al., 2022a). In fact, the drone enables overall photos of the skeletons to be taken from a consistent height, which is difficult to achieve with simple ladders or elevators, leading to excellent 3D resolution even of the dorsal parts of the specimens that are often difficult to reach.

The values obtained by applying the regression method underline the significant variability of BM estimates calculated using different methodological approaches based on long-bone dimensions, as well as applying the same methodological approaches to different bones even belonging to the same individual (i.e. *A. arvernensis* from Ca′ dei Boschi) (Figure 12, Table 1). For instance, some inconsistencies can indeed be observed when comparing the BM values obtained for each variable of the forelimb bones in the two skeletons (Figure 12). The comparison between the BM estimates derived from the dimensions of forelimb bones of *A. arvernensis* from Ca′ dei Boschi and Montecarlo (Figure 12) highlights, on the one hand, the differences, sometimes significant, among the BM values derived from each variable, and, on the other hand, some uniformity in the trend of such differences between the BM values obtained for the two specimens, with the BM values returned for the Val skeleton that are on average slightly higher than those calculated for the VA individual.

Some BM estimates derived from the distal articular surface of the humerus, such as H-lcw, H-dist.art and especially H-mcl, deviated from this pattern and returned a BM value that was significantly higher in the VA specimen than the Val specimen (note, however, that it might be difficult to take these measurements on mounted skeletons). In particular, comparing the results obtained by analysing samples VA-B and Val-B, H-lcw corresponds to the minimum BM average value obtained for the VA sample and to a BM value close to the average BM value for the Val one.

The VA and Val BM patterns shown by the best six variables are substantially coherent, with the BM obtained for the Val bone measurements slightly exceeding those of the VA corresponding measurements except for the maximum lengths of the diaphragm and humerus, which were nearly the same in both specimens and returned an almost equal BM value (Figure 12).

Some differences can also be detected when comparing the average BM values obtained using Christiansen's (2004) formulas of the BM value samples calculated on all the variables with those derived from the best variable, though the difference decreases when comparing the average BM of forelimb bones (Figure 13). The differences became much more evident when comparing the average BM values obtained by applying different methods, which show roughly the same pattern in VA and Val data samples. The BM values derived for the Montecarlo specimens are higher than those of the Ca′ dei Boschi individual, except for the values calculated from the shoulder height that are fully comparable (Figure 13).

All things considered, we could assume that the average BM obtained for the Ca′ dei Boschi and Montecarlo *A. arvernensis* specimens using linear long-bone dimensions possibly ranges from about 4 to 6 t, with a hypothetical average value of about 5 t and 5.5 t for the *A. arvernensis* skeletons from Ca′ dei Boschi and Montecarlo, respectively.

The comparison between the results obtained with the regression formulas just discussed and the volumetric method is clear in the box plots of Figure 14. Both in the specimens from Montecarlo and from Ca′ dei Boschi, the BM range obtained through the regression formulas is always greater when compared with the results of the volumetric method. In particular, a greater range was obtained by applying the Christiansen (2004) formulas with values ranging from a minimum of 54 kg (excluding the really too low results of the fibula) to a maximum of about 25 t in the Villafranca specimen, and from 75 kg to a maximum of about 9.5 t in the Montecarlo specimen. The second largest range in both skeletons was obtained by applying the universal formula of Campione and Evans (2012), with values from a minimum of 3.2 t to a maximum of 6.3 t in the Villafranca specimen, and from 3.4 to 6.7 t in the Montecarlo skeleton. Differently, the range calculated by applying the formula based on shoulder

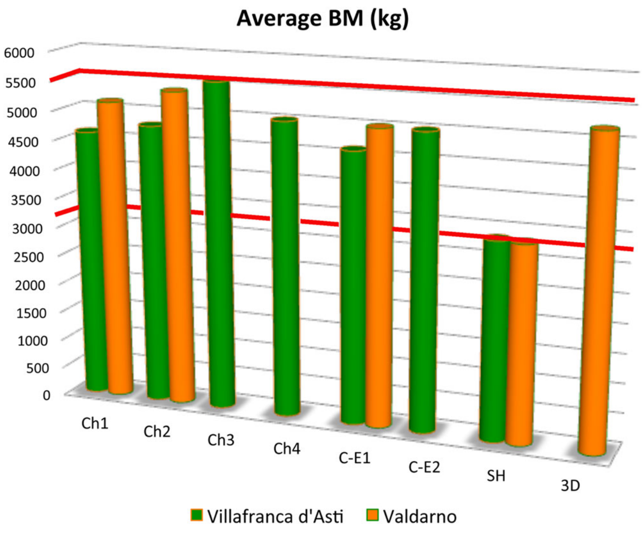

Figure 13. Comparison among the average BM estimates obtained, using different methodological approaches from the forelimb long-bone dimensions of *Anancus arvernensis* specimens from Villafranca d'Asti (Capellini Palaeontological Museum, Bologna) and Valdarno (Geological and Palaeontological Museum, Florence) (Ch1, Ch2, C-E1, SH and 3D) and from the forelimb long-bone dimensions of *Anancus arvernensis* specimens from Villafranca d'Asti. CH, and C-E = methods proposed by Christiansen (2004) and Campione and Evans (2012), respectively; SH = BM estimates based on shoulder height (Larramendi, 2015, 2016); 3D = BM estimates based on 3D models (Romano et al., 2019, 2022); Ch1, and Ch2 = BM obtained by averaging the BM values derived from all and the best six forelimb long-bone dimensions, using Christiansen's (2004) regression equations. [Color figure can be viewed at wileyonlinelibrary.com]

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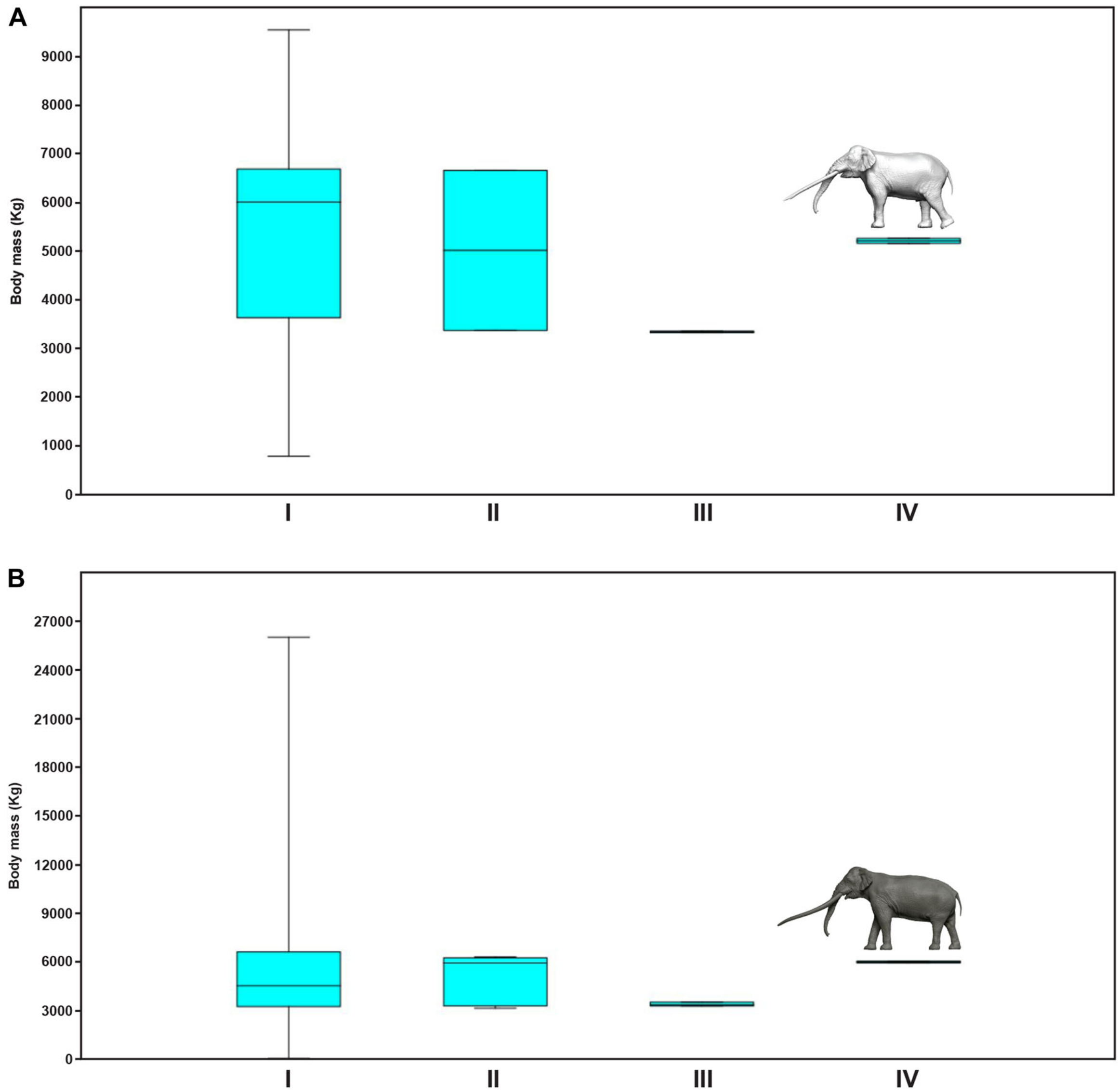

Figure 14. Box plots relating the ranges of the BM estimate obtained with the volumetric method and with traditional regression methods based on the specimen from the Geological and Palaeontological Museum, Florence (A) and from Capellini Palaeontological Museum, Bologna (B). (I) Values obtained using Christiansen (2004); (II) values obtained using Campione and Evans (2012); (III) values obtained using Larramendi (2016); (IV) volumetric method presented in the present work. [Color figure can be viewed at wileyonlinelibrary.com]

height by Larramendi (2016) is very limited in both specimens, and the same can be observed in the results obtained with the new 3D volumetric approach (Figure 14).

Taking into account the average volumetric BM as the closest figure to the natural condition, some interesting considerations can be made regarding the results obtained with the regression formulas based on single skeletal measurements or their combinations. Concerning the specimen from Villafranca, it is interesting to note how, despite the large range of values obtained, the average of all estimates is very close to the volumetric average (5559 vs 6000 kg), with an underestimation of only 7%. By contrast, considering the single estimates, we obtain an underestimation of 99% to an overestimation of up to 334%. Similarly, the average calculated using the Campione and Evans (2012) method does not differ much from the volumetric average (5011 vs 6000 kg), with an underestimation of about 16%. Considering the individual formulas differently, the method by Campione and Evans (2012) returns a maximum underestimation of 47% and a maximum overestimation equal to 5%. The method of Larramendi (2016) based on the shoulder height, though providing a very narrow range, underestimates the BM in both specimens, with an average underestimation equal to 43% for the Villafranca skeleton and of 44% for the Montecarlo specimen. The same general results are obtained for the specimen from Montecarlo, with the only difference represented by a lower range in the regression formulas estimate, due exclusively to fewer bones being available for calculations (hindlimb not preserved).

For all the above, and considering the Villafranca specimen as more representative, being more complete, this contribution showed how Christiansen's (2004) method can return plausible BM estimates only when the average of all the formulas on the individual bones is available and considered. Conversely, the application of the formulas to fragmented skeletons or worse to single bones can lead to highly misleading results and overestimates of even more than 300%. In particular, the fibula and tibia were shown to be the osteological elements less able to predict the BM in *Anancus*, whereas fairly consistent results were obtained using the circumference of the humerus, ulna, radius and femur. This element once again shows, as already proposed in the literature (e.g. Anderson et al., 1985; Campione and Evans, 2012) that the section and circumference of the long bones are among the best predictors of BM, being more

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connected to the support of body weight both during locomotion and resting phases. By contrast, overestimations of more than 200% have been obtained using formulas based on the lengths of the condyles in the humerus and femur, the results of which are therefore of little value for the estimation of the BM, at least for the genus *Anancus*. Similar results have also been recently obtained for the circumference of the ulna and femur in *Mammuthus meridionalis* (Romano et al., 2022b), returning plausible values quite close to the volumetric ones; however, in that case the circumference of the humerus returned an overestimated BM value of about 23%, probably due to the very robust and 'overbuilt' structure (*sensu* Romano, 2017; Romano and Rubidge, 2019a) of the anterior stylopodium in the taxon.

Conclusions

In the present contribution, we explored the possible living BM of the anancine gomphotheriid *A. arvernensis*, comparing the traditional methods based on regression formulas with a new volumetric approach recently proposed for extinct tetrapods. The study, conducted using two articulated skeletons, demonstrated that the accuracy of regression formulas in estimating BM varies significantly across taxa, even within the same clade. Body mass results indicate that plausible estimates can be obtained only when the mean of all the formulas applied to individual bones is taken into account. Conversely, formulas applied to single bones can result in underestimations or overestimations of up to 300%, with estimated body masses ranging from 54 kg to 26 t, values that are entirely implausible for a proboscidean of those dimensions. These inconsistent results are probably due to the general structure of long bones in extinct tetrapods, which exhibit proportions that are sometimes significantly different from the conditions characterising extant taxa used to derive regression formulas. In particular, previous studies have shown that many of these bones appear to be 'overbuilt' (*sensu* Romano, 2017; Romano and Rubidge, 2019a), meaning they are more robust and have larger circumferences than would be expected to support a given body weight. In taxa with a primitive sprawling posture and large body masses, this more robust structure may be explained by greater torsional forces compared with a posture with columnar limbs. Currently, there are no tetrapods with a sprawling posture that exceed one tonne in weight, so it is quite evident that regression formulas based on living taxa show a substantial bias in this regard.

Differently, by employing the new volumetric approach, a reconstruction of a more solid and plausible body mass of *A. arvernensis* was made possible, resulting in an estimated BM of 5.2 to 6 t, which is similar to that of a mature male African elephant.

For all the above, the use of single or fragmentary bones for BM estimates of terrestrial tetrapods is therefore strongly discouraged, also for tetrapods with current analogues that are fairly close, such as proboscideans. Calculations based on single bones should be strongly avoided especially if for the purpose of macro-evolutionary analyses, since they can lead to highly implausible and misleading results. Also, in this case the volumetric method based on an *in vivo* 3D reconstruction yielded a more sound and solid BM estimate, reflecting the natural condition for a proboscidean of that size, and is thus always preferable and to be recommended if sufficiently complete mounted skeletons are available.

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Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

Supporting information

Additional supporting information can be found in the online version of this article.

Abbreviations. %PE, per cent prediction error; %SEE, per cent standard error of the estimate; BM, body mass; CPMBo, Capellini Palaeontological Museum (Bologna); DIAPReM, Centro Dipartimentale per lo Sviluppo di Procedure Automatiche Integrate per il Restauro dei Monumenti; dx, right; F-circ., femur least circumference of dyaphisis; Fi-circ., fibula least circumference of dyaphisis; F-diap.ap, femur diaphysial diameter in the anteroposterior plane; F-diap.lm, femur diaphysial diameter in the lateromedial plane; F-dist.art, femur width of distal articular surface; Fi-diap.ap, fibula diaphysial diameter in the anteroposterior plane; Fi-diap.lm, fibula diaphysial diameter in the lateromedial plane; Fi-length, fibula maximum length; F-lcl, femur lateral condyle length; F-lcw, femur: lateral condyle width; F-length, femur: maximum length; F-mcl, femur medial condyle length; F-mcw, femur medial condyle width; GPMFi, Geological and Palaeontological Museum (Florence); H-circ., humerus least circumference of dyaphisis; H-diap.ap, humerus diaphysial diameter in the anteroposterior plane; H-diap.lm, humerus: diaphysial diameter in the lateromedial plane; H-dist.art, humerus: width of distal articular surface; H-lcl, humerus: lateral condyle length; H-lcw, humerus: lateral condyle width; H-mcl, humerus: medial condyle length; H-mcw, humerus: medial condyle width; r, regression coefficient; R-circ., radius least circumference of dyaphisis; R-diap.ap, radius diaphysial diameter in the anteroposterior plane; R-diap.lm, radius diaphysial diameter in the lateromedial plane; R-length, radius maximum length; SH1, skeletal height at the shoulder, corresponding to 95% of the sum of the bone maximal length; SH2, physiological height at the shoulder, corresponding to 98% of the sum of the bone articular length; sSH, height at the shoulder; sx, left; T-circ., tibia least circumference of dyaphisis; T-diap.ap, tibia diaphysial diameter in the anteroposterior plane; T-diap.lm, tibia diaphysial diameter in the lateromedial plane; T-length, tibia maximum length; U-circ., ulna least circumference of dyaphisis; U-diap.ap, ulna diaphysial diameter in the anteroposterior plane; U-diap.lm, ulna diaphysial diameter in the lateromedial plane; U-length, ulna: maximum length; VA, A. arvernensis skeleton at Museum of Geology and Palaeontology 'Giuseppe Capellini' (University of Bologna, Italy); VA-A and Val-A, specimen which include all of the BM estimates obtained from the long bones of the fore and hindlimbs of VA and the long bones of the forelimb of the Val specimen; VAB and Val-B, specimen which include the BM values selected after removing BM values that are too high or too low for animals with a size comparable to that of Anancus adult representatives; VA-C and Val-C, sample which include only the variables used in the equations that have the highest regression coefficient; VA-D, sample with all the variables; VA-E, sample with selected variables; VA-F, best six variables.; VAL, A. arvernensis skeleton at Museum of Geology and Palaeontology of the University of Florence (Italy).

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