Tooth and long bone scaling in Sardinian ochotonids (Early Pleistocene-Holocene): Evidence for megalodontia and its palaeoecological implications

Blanca Moncunill-Solé [a,b,1,*], Caterinella Tuveri [c], Marisa Arca [c], Chiara Angelone [a,d,e]

[a] *Dipartimento di Scienze, Università degli Studi Roma Tre, 00146 Roma, Italy*
[b] *Departamento de Física e Ciencias da Terra, Universidade da Coruña, 15008 A Coruña, Spain*
[c] *Soprintendenza Archeologia, Belle Arti e Paesaggio Per le Prov. di Sassari e Nuoro, 08100 Nuoro, Italy*
[d] *Institut Català de Paleontologia Miquel Crusafont (ICP), Campus de la Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Spain*
[e] *Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Palaeoanthropology, Chinese Academy of Sciences, 100044 Beijing, China*

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ABSTRACT

Body size is a useful character to unravel the biology of fossil taxa and, indirectly, the palaeoenvironment in which they lived. However, the reliability of size proxies is debated, particularly among insular endemics in which large teeth relative to body size have been observed. To shed light on this issue, here we compute statistical models to assess: (i) teeth and long bone scaling and (ii) dentition size evolutionary dynamics in the anagenetic lineage *Prolagus figaro-P. sardus* from the late Early Pleistocene-Holocene of Sardinia, Italy. Postcranial bones, particularly tibial epiphyses, are shown to be the most suitable parameters for prediction of body mass in *Prolagus* and other lagomorph taxa. By contrast, p3 should not be used for size reconstructions, whereas m1 width provided the highest correlation with long bones. On the other hand, the postcanine occlusal surface of Sardinian *Prolagus* (m1 and toothrow area) appeared significantly larger than those of extant lagomorphs, pointing to a higher resistance to tooth wear and a more durable permanent dentition. It seems likely that megalodontia might have evolved in Sardinian *Prolagus* to cope with the abrasive diet found on islands (food habit hypothesis). Nonetheless, we cannot exclude that other biological features, such as long longevity, could be co-driving forces in this fossil lineage (life history hypothesis). The results achieved throw light on size and scale evolution in lagomorphs, as well as refine the eco-evolutionary responses of small mammals to insular regimes.

1. Introduction

Body mass (BM), a proxy of size, has a central position in the immense network of biological variables of organisms. It is correlated with an extensive set of morphological, behavioral, physiological, ecological and life history traits (Peters, 1983; Calder III, 1984; Schmidt-Nielsen, 1984) and, ultimately, it has a decisive role in the evolution of organisms (Purvis and Orme, 2005). In this regard, the weight estimations of extinct species provide essential clues to understand their palaeobiology, as well as their roles in palaeocommunities and palaeoenvironments (Palombo, 2009; Lyras et al., 2010; van der Geer et al., 2013; Lomolino et al., 2013; Moncunill-Solé et al., 2014, 2016a, 2016b;

Moncunill-Solé, 2021). Historically, the BM of extinct lagomorphs were estimated using rodent regression curves (Deng, 2009), although descriptions of these methodological procedures were rarely provided. In recent years, the body size evolution of fossil lagomorphs has evoked great scientific interest, and accurate BM regression models have been developed and used in this mammalian order (Quintana Cardona, 2005; Quintana et al., 2011; van der Geer et al., 2013; Quintana Cardona and Moncunill-Solé, 2014; Moncunill-Solé et al., 2015, 2016a, 2016b; Winkler et al., 2016; Moncunill-Solé, 2021).

To deepen the knowledge of the Island Rule in small mammals (generalities, mechanisms, and drivers), the BM variation of the anagenetic lineage of *Prolagus* from Sardinia, Italy (*Prolagus figaro* López

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Martínez in López Martínez and Thaler, 1975 - *P. sardus* [Wagner, 1829]) was addressed. Angelone et al. (2008) described an evolutionary asymptotic size increase, considering teeth and bones from several sites located in Monte Tuttavista (Orosei, Italy). Eventually, Moncunill-Solé et al. (2016a) considered the size variation of the lower third premolar (p3) and long bones (femur, humerus and tibia) in correspondence with the turnover in which the Middle Pleistocene-Holocene species *P. sardus* replaced its ancestor, the latest Pliocene/earliest Pleistocene-late Early Pleistocene species *P. figaro*. The authors provided evidence of a progressive BM increase during the anagenetic lineage, but also identified wide discrepancies between teeth and long bones as BM proxies. Similar inconsistencies have also been observed in other taxa, and a strong debate is ongoing with regard to the reliability of size proxies in extinct species (Gould, 1975; Jungers, 1990; Millien and Bovy, 2010; Moncunill-Solé et al., 2015). Especially in the case of insular endemics, researchers have noted large teeth relative to body size in extinct taxa, but this issue has not been studied in detail (Maglio, 1973; Moyà-Solà and Köhler, 1997; Angelone, 2005; Moncunill-Solé et al., 2015, 2016a).

A decade after the publication of the first regression models for estimating the size of extinct lagomorphs and in view of the above, a statistical review is required. In this regard, the present study has two main objectives: (i) to assess the scaling relationship among skeletal elements (teeth and long bones) and to determine the validity and reliability of these features as size proxies in the order Lagomorpha; (ii) to evaluate the evolutionary trends of dentition size to BM in an extinct insular lagomorph. The long-lasting lineage *P. figaro - P. sardus* from Sardinia (Early Pleistocene-Holocene) is considered the most suitable taxon for carrying out the present research. This lineage stands out for recording significant morphological and dimensional variations in its dental and osteological components, and the remains (teeth and bones) of both species are extremely abundant, well preserved, and quite easy to identify from the rest of the fossil small mammal assemblage. The results of the present study will contribute to improving the biological knowledge of fossil lagomorphs and to understanding the size diversity and the scale variations of this mammalian order. In addition, they will shed light on the eco-evolutionary dynamics of small mammals in insular regimes.

2. Material and methods

2.1. Material

A total of 2997 isolated fossil elements belonging to *P. figaro* and *P. sardus* were assessed, including teeth (p3 and m1), hemimandibles, and postcranial bones (femora, humeri and tibiae) of adult individuals (Table 1, S1). It was impossible to identify teeth and bones from the same specimen, because in the field the remains were not in anatomical position. The study did not consider sexual size dimorphism due to lack of such kind of differences in extant and extinct lagomorph taxa (Lu et al., 2014; Pelletier, 2019).

The remains were retrieved from 9 fossiliferous sites of Sardinia (Italy): the fissures infillings X3, X4, XIr, VIb6 of the Monte Tuttavista karstic complex (Orosei), Cava Alabastro (Fluminimaggiore), Grotta dei

Fiori SD (Carbonia), Grotta Teulada (Teulada), Dragonara cave (= Grotta della Medusa; Alghero), and S'Omu e S'Orku (Arbus) (Fig. 1A) (Gliozzi et al., 1984; Abbazzi et al., 2004; Floris et al., 2009; Boldrini et al., 2010; Palombo and Rozzi, 2014; Palombo et al., 2017). For details about the stratigraphy and the faunal assemblages relative to the above mentioned fossil sites, see Boldrini (2009) and references therein. The Monte Tuttavista fissures infillings X3 and X4 are correlated to the Capo Figari/Orosei 1 faunal subcomplex of the *Nesogoral* Faunal Complex and to the Orosei 2 faunal subcomplex of the *Microtus* (*Tyrrhenicola*) Faunal Complex (latest Pliocene to late Early Pleistocene). The Monte Tuttavista fissures infillings XIr and VIb6, Cava Alabastro, Grotta dei Fiori SD, Grotta Teulada and Dragonara Cave belong to the Dragonara faunal subcomplex of the *Microtus* (*Tyrrhenicola*) Faunal Complex (Middle Pleistocene to Holocene). Absolute dates are available for Dragonara Cave (22.39–21.91 ka) and S'Omu e S'Orku (8.7–8.5 ka) (Fig. 1B) (Palombo et al., 2017; Zoboli et al., 2018).

The studied material is curated in the Soprintendenza dei Beni Archeologici per le Province di Sassari e Nuoro (Nuoro, Sardinia, Italy) and the Laboratory of Vertebrate Palaeontology of the Department of Science, Università degli Studi Roma Tre (Roma, Italy). A detailed list of extant lagomorph species (ochotonids and leporids), with associated data (sample size, collection, and reference), used for comparative purposes is provided in Supplementary Data (Appendix A).

2.2. Measurements

Teeth were measured using a Leica MZ6 modular stereomicroscope combined with a digital camera Leica DFC290. The following measurements were taken: p3 width (**Wp3**), p3 length (**Lp3**), m1 width (**Wm1**), m1 length (**Lm1**) and length of lower toothrow (**TRL**) (Fig. 2A-C) (López-Martínez, 1989; Quintana Cardona, 2005; Quintana and Agustí, 2007; Hordijk, 2010; Moncunill-Solé et al., 2015). Values of the areas of the occlusal surface of p3 (**p3AA** = Lp3 x Wp3), m1 (**m1AA** = Lm1 x Wm1), and lower toothrow (**TRLAA** = Wm1 x TRL) were subsequently calculated (Moncunill-Solé et al., 2015). On postcranial bones, the following measurements were taken with a manual caliper: humerus length (**HL**), proximal humeral antero-posterior diameter (**HAPDp**), distal humeral transversal diameter (**HTDd**), distal humeral antero-posterior-diameter (**HAPDd**), femur length (**FL**), proximal femoral transversal diameter (**FTDp**), distal femoral transversal diameter (**FTDd**), tibia length (**TL**), proximal tibial antero-posterior diameter (**TAPDp**), proximal tibial transversal diameter (**TTDp**), and distal tibial transversal diameter (**TTDd**) (Fig. 2D-F) (Quintana Cardona, 2005; Moncunill-Solé et al., 2015).

The above listed measurements are commonly used for predicting the size of extinct lagomorphs and they lack taxonomic value (Quintana Cardona, 2005; Moncunill-Solé et al., 2015). The specific differentiation between the two Sardinian ochotonids (*P. figaro* and *P. sardus*) is based on the morphology and complexity of the p3 enamel (López Martínez and Thaler, 1975). Other postcranial elements, such as proximal tarsals, are considered good BM proxies in mammals (Tsubamoto, 2014). However, they were found in low amounts in the studied fossiliferous sites, and the few recovered were in poor conditions.

Table 1

Number of assessed remains belonging to *P. figaro* and *P. sardus*. Last column and row indicate the total material per element and site respectively.

| Element | | Sites | | | | | | | | | |
		X3	X4	Cava Alabastro	XIr	Grotta dei Fiori SD	Grotta Teulada	VI banco 6	Dragonara cave	S'Omu e S'Orku	Total
Teeth	p3	7	161	33	52	9	7	51	54	82	456
	m1	1	51	33	135	16	5	0	141	111	493
	Lower toothrow	0	15	15	108	8	6	0	146	119	417
Postcranial	Humerus	14	0	53	57	33	11	45	347	167	727
	Femur	14	13	7	68	10	17	19	178	73	399
	Tibia	5	11	14	39	6	6	9	375	40	505
Total		41	251	155	459	82	52	124	1241	592	2997
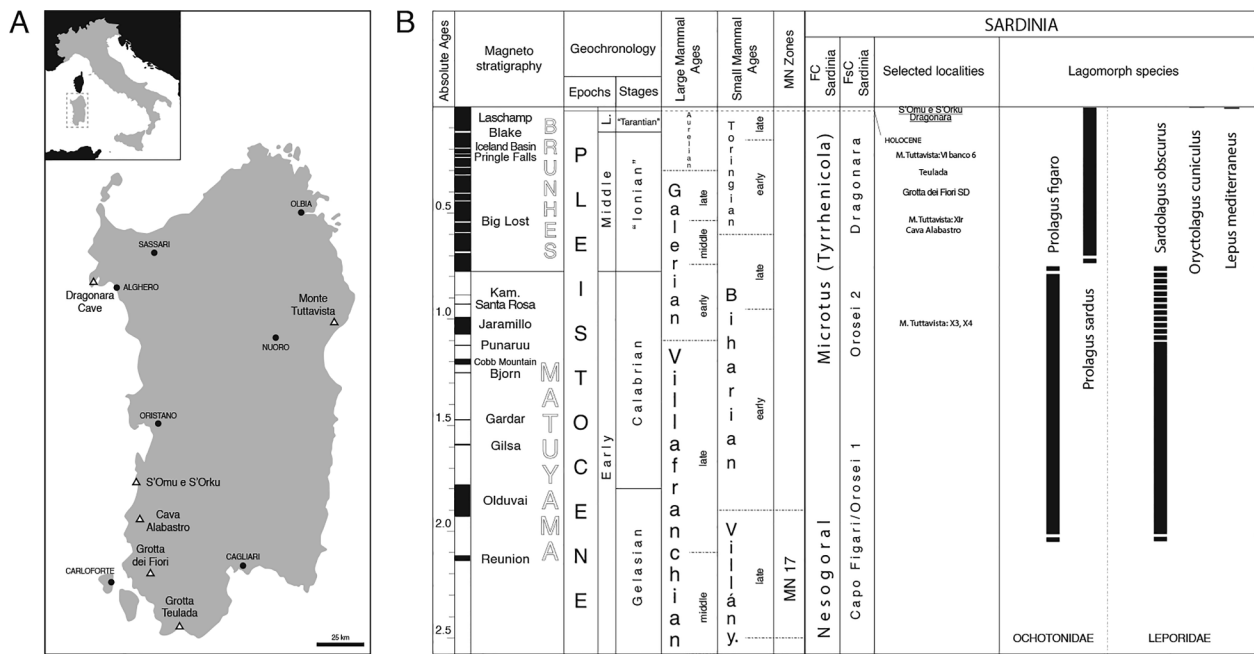
Fig. 1. A, Sardinian location map (Italy) showing the studied fossiliferous sites (white triangles) and the main cities (black dots). Data derive from Gliozzi et al. (1984), Abbazzi et al. (2004), Floris et al. (2009), Melis et al. (2013), Palombo and Rozzi (2014), and Palombo et al. (2017). Study sites are protected but exact location information will be shared with qualified researchers upon request. B, Chronological distribution of Sardinian lagomorph taxa, based on Angelone et al. (2020). Chronological position of fossil sites derives from Palombo (2009), Palombo and Rozzi (2014) and Zoboli et al. (2018). Those underlined have been absolute dated, whereas the others have a relative position.

2.3. Scaling analysis

Following the elastic similarity model (ESM), McMahon (1973, 1975) proposed that limb bone lengths (L) should scale to $BM^{1/4}$, whereas limb bone diameters (D) or least circumferences should do to $BM^{3/8}$. In artiodactyls (especially in ungulates), this model was fitted suitable, but the empirical data of other taxa suggested geometric similarity (L α D α $BM^{1/3}$) (Alexander et al., 1979; Biewener, 1983; Garcia and da Silva, 2006 and references therein). When the size of specimens was considered a critical factor, results showed that long bones of small mammals (BM < 20 kg) were geometrically similar and those of large mammals followed ESM (Economos, 1983; Christiansen, 1999a). Twenty years later, Garcia and da Silva (2004, 2006) proposed a new scaling model which considered that bending and compressive stresses were the forces that governed long-bone allometry. Accordingly, L and D should scale to $BM^{0.37}$ in small-sized mammals. On the other hand, there is an historical debate about teeth area scaling. Following geometric similarity model, areas should scale to $BM^{2/3}$. Gould (1975), alternatively, suggested that postcanine occlusal area (PCOA ≈ TRLAA), which was directly related to food processing and mammal's metabolic needs, should scale as basal metabolic rate did (PCOA α $BM^{3/4}$). However, empirical evidences showed different relationships among the taxa. The results obtained for rodents pointed to geometric similarity, but similar analyses were never tested in rabbits, hares, or pikas (Copes and Schwartz, 2010). Moncunill-Solé et al. (2015) have carried out the most complete scaling study based on extant lagomorphs, assessing 12 species of ochotonids and 36 of leporids. Their results showed that teeth linear dimensions of ochotonids scale to 0.37 (Lm1 α $BM^{0.37}$, Wm1 α $BM^{0.38}$ and TRL α $BM^{0.36}$) and areas to 0,71 (m1AA α $BM^{0.70}$, TRLAA α $BM^{0.72}$). On the other hand, they found that in long bones L α $BM^{0.43}$ and D α $BM^{0.39}$ in lagomorphs.

For the assessment of scaling, the first step was to carry out a statistical descriptive analysis of the morphometric variables. The normality (Shapiro-Wilk test) and the homogeneity of variances (Levene's test) were also assessed. Arithmetic averages of morphometric measurements were calculated for the 9 studied fossiliferous sites. The use of means is a common procedure carried out in historical and cutting-edge allometric investigations for not biasing the sample (Peters, 1983; Calder III, 1984; Schmidt-Nielsen, 1984; Christiansen, 1999b; Copes and Schwartz, 2010; Millien and Bovy, 2010). Data were log transformed for analysis. The relationships among linear dimensions of teeth (L and W) and postcranial bones (L and D) were assessed by means of correlation tests: Pearson correlation coefficient (r, parametric statistics) and Spearman correlation coefficient (ρ, non-parametric statistics), which range from −1 to 1. Extreme scores (−1 or + 1) indicate a perfect linear relationship (negative or positive respectively), whereas score of 0 means no relationship. Area variables (p3AA, m1AA and TRLAA) were not considered in this assessment, because original ones (L and W) are tested.

Bivariate linear regression tests (Ordinary Least Squares, OLS, Model I) are used in allometric studies to examine the dependency degree of variables and their scaling relationship (Christiansen, 1999b). This test was only carried out on those variables that showed significant correlation relationships. This methodology allowed to find the line (equation) that describes the variables' relationship with the smallest error. The result is an eq. $Y = a + bX$, where Y is the dependent variable, a is the intercept with the y-axis, b is the slope, and X is the independent variable. Scaling relationship was evaluated by means of slope values. $b = 1$ indicates an equal growth rate of variables (isometry), whereas $b \neq 1$ suggests an allometric relationship (positive or hyperallometric when $b > 1$, and negative or hypoallometric when $b < 1$) (Huxley and Teissier, 1936). We evaluated b considering its 95% bootstrapped confidence intervals (CI) ($N = 1999$). Isometry was established when CI comprised the value 1, whereas allometry (negative or positive) was established when this value was not included.

In addition, multiple regressions ($Y = a + b_1X_1 + b_2X_2 + ... + b_kX_k$; where k is the total number of independent variables) were carried out using Partial Least Square Regression (PLS or PLSR) models. This data-dimension reduction test was considered suitable in the present case because the number of variables was higher than number of cases (Höskuldsson, 1988). This technique reduces the number of predicting variables to a set of components (orthogonal factors, predictors), which
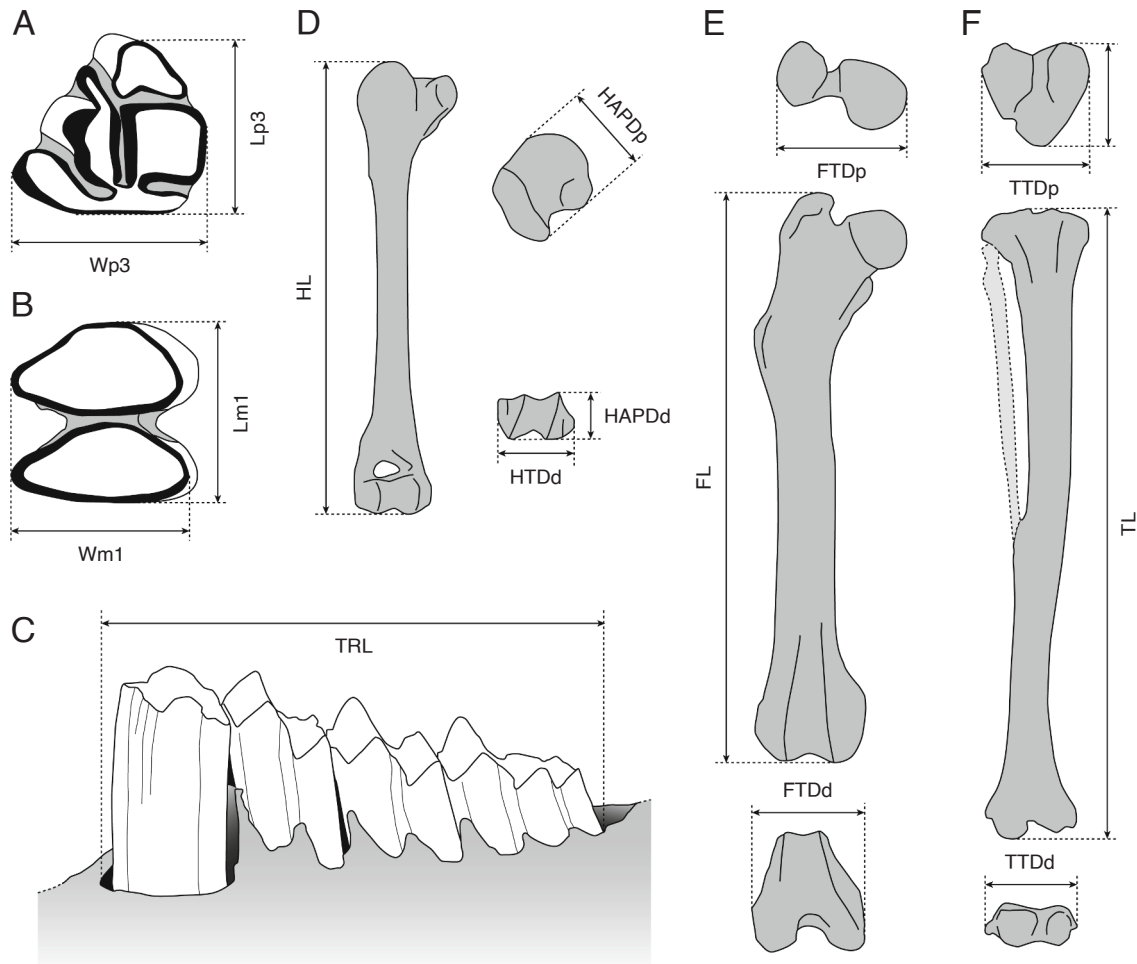
Fig. 2. Measurements taken on *Prolagus* remains. A, p3: Lp3, length of p3; Wp3, width of p3. B, m1: Lm1, length of m1; Wm1, width of m1. C, hemimandible: TRL, toothrow length. D, humerus: HL, humerus length; HAPDp, proximal humeral antero-posterior diameter; HAPDd, distal humeral antero-posterior diameter; HTDd, distal humeral transversal diameter. E, femur: FL, femur length; FTDp, proximal femoral transversal diameter; FTDd, distal femoral transversal diameter. F, tibia: TL, tibia length; TAPDp, proximal tibial antero-posterior diameter; TTDp, proximal tibial transversal diameter; TTDd, distal tibial transversal diameter. Illustrated material belongs to *P. sardus* from Dragonara cave.

describe the maximum correlation between explanatory and response variables, and, in addition, removes the multicollinearity (Mateos-Aparicio Morales and Caballero Domínguez, 2009; Šerbetar, 2012). This test was fitted using the R package "*plsdepot*" (Sánchez, 2016).

The significance level of all mentioned tests was fixed at 0.05. This statistical methodology is extensively described in Quinn and Keough (2002) and McDonald (2014). All the analyses were performed using the software Jamovi version 0.9.2.3 (The Jamovi Project, 2019), Past 3.25 (Hammer et al., 2001) and R 3.6.1. (R Core Team, 2019).

2.4. Teeth size index (TSI)

Teeth size indices were calculated to evaluate evolutionary trends in the dentition of Sardinian *Prolagus*. They were based on the postcanine megalodontia (= megadontia) quotient established by McHenry (1988) in the study of extinct primates and early hominins. This index was calculated considering: (i) the area of lower premolars and molars (TRLAA):

$$\text{TSI}_{\text{TRLAA}} = \frac{\text{observed TRLAA}}{\text{predicted TRLAA from the BM}}$$

and (ii) the area of the m1 (m1AA, teeth that showed the highest correlation coefficient and significant dependency with postcranial bones,

see results Section 3.2. for details):

$$\text{TSI}_{\text{m1AA}} = \frac{\text{observed m1AA}}{\text{predicted m1AA from the BM}}$$

Values of TSI > 1 indicate an increase of teeth size compared with the average (control) extant species (= megalodontia); whereas values of TSI < 1 mean microdontia. Predicted teeth areas of extinct populations were obtained using the allometric models described by Moncunill-Solé et al. (2015), which were established independently by extant ochotonids (log BM = 0.566 + 1.397 log TRLAA and log BM = 1.454 + 1.418 log m1AA) and leporids (log BM = 0.462 + 1.659 log TRLAA and log BM = 1.890 + 1.470 log m1AA). The BM of each specimen was calculated using tibial diameters (TAPDp, TTDp and TTDd), which are the parameters that show the best correlation with BM in *Prolagus* (see present results, Moncunill-Solé et al., 2016a).

ANCOVA tests were used to evaluate statistically the m1AA and TRLAA differences among groups adjusted for the size (covariate: BM, TAPDp, TTDp and TTDd). Data were log transformed for analysis. The established categories or groups (fixed factor) were: (i) Sardinian *Prolagus*, (ii) extant ochotonids, and (iii) extant leporids (Supplementary Data, Appendix A). Whilst it would be interesting to consider mainland *Prolagus* species in the study, the general absence of their long bones (poor and in bad conditions) prevents it. The significance level was fixed

at 0.05 and the tests were carried out using the software Jamovi version 0.9.2.3 (The Jamovi Project, 2019).

3. Results

3.1. Descriptive analysis

The material of *Prolagus* analyzed in this paper was not fairly distributed among sites. Dragonara, the richest assemblage, provided more than 1200 fossils, whereas in other localities the number of remains was significantly lower (e.g. X3 or Grotta Teulada) (Tables 2–5). The relative abundance of each bone/teeth was not uniform either. In general, the most frequently recovered bone was the humerus, in particular those in which distal epiphysis was preserved (Table 3). Regarding teeth, in some cases p3 was the most abundant (X4 or VIb6), but in other sites m1 predominated (XIr or S'Omu e S'Orku) (Table 2).

X3 and Grotta dei Fiori SD localities were characterized by the smallest teeth dimensions (p3 and m1), whereas the largest ones were retrieved from Dragonara. Considering TRL, the specimens from Grotta dei Fiori SD, XIr and Grotta Teulada were the smallest and S'Omu e S'Orku ones the largest (Table 2). The smallest humeral values were observed in Cava Alabastro specimens and the largest ones in VIb6, Dragonara and S'Omu e S'Orku (Table 3). By contrast, Cava Alabastro and Dragonara individuals showed the largest femora, whereas those from VIb6, X3 and X4 the smallest (Table 4). In the case of tibia, it was observed a stable pattern in all the assessed variables: X3 specimens had the smallest values and those from Dragonara the largest (Table 5).

It is worth to notice that some variables did not follow a normal distribution (e.g. humerus variables), and/or their variances were not homogenous among groups (e.g. p3 variables) (Tables 2–5, Supplementary Data, Appendix A). In these cases, the subsequent statistical tests were non-parametric. Also noteworthy is that some histograms seem not to be unimodal distributions (Supplementary Data, Appendix A), but they probably result from the low number of specimens examined in these populations (e.g. X3 or Grotta dei Fiori SD).

Table 3

Humerus measurements (in mm) of *P. figaro* and *P. sardus* per fossiliferous site: mean, standard deviation (SD) and number of specimens (N).

			HL	HAPDp	HTDd	**HAPDd**
Prolagus figaro	X3	Mean	35.80	8.36	6.51	3.66
		(SD)	(2.530)	(0.826)	(0.631)	(0.404)
		N	5	7	12	12
	X4	Mean	–	–	–	–
		(SD)				
		N	0	0	0	0
	Cava Alabastro	Mean	34.30	–	5.94	3.38
		(SD)	(1.150)		(0.417)	(0.228)
		N	3	0	43	53
	XIr	Mean	38.20	8.82	6.59	3.87
		(SD)	(1.480)	(0.577)	(0.360)	(0.215)
		N	47	42	53	54
Prolagus sardus	Grotta dei Fiori SD	Mean	39.10	8.30	6.11	3.53
		(SD)	(2.820)	(0.707)	(0.457)	(0.365)
		N	3	2	31	32
	Grotta Teulada	Mean	–	–	6.21	3.51
		(SD)			(0.561)	(0.398)
		N	0	0	7	7
	VI banco 6	Mean	38.70	8.98	6.63	3.92
		(SD)	(1.730)	(0.696)	(0.341)	(0.246)
		N	44	41	44	44
	Dragonara cave	Mean	39.80	8.64	6.81	4.03
		(SD)	(1.940)	(0.570)	(0.462)	(0.315)
		N	48	57	318	334
	S'Omu e S'Orku	Mean	45.00	7.93	6.44	3.69
		(SD)	(6.360)	(0.833)	(0.429)	(0.311)
		N	2	3	152	158

Variables with a non-normal distribution are underlined, while those without homogeneity of variances among groups are in bold. See ages of fossil sites in Table 2.

3.2. Correlation, bivariate regression and PLS analyses

The study showed significant correlations ($p < 0.05$) among some of the assessed variables (Fig. 3), as well as dependency (Table 6;

Table 2

Teeth measurements (in mm) of *P. figaro* and *P. sardus* per fossiliferous site: mean, standard deviation (SD) and number of specimens (N).

			Lp3	Wp3	p3AA	Lm1	Wm1	m1AA	TRL	TRLAA
Prolagus figaro	X3[1]	Mean	2.11	1.86	4.01	2.73 (−)	2.43 (−)	6.62 (−)	–	–
		(SD)	(0.383)	(0.272)	(1.280)					
		N	7	7	7	1	1	1	0	0
	X4[1]	Mean	2.59	2.53	6.53	2.52	2.75	6.95	12.50	34.80
		(SD)	(0.320)	(0.322)	(1.520)	(0.228)	(0.284)	(1.250)	(0.678)	(5.320)
		N	151	141	130	51	44	44	15	12
	Cava Alabastro[2]	Mean	2.77	2.85	7.90	2.45	2.80	6.94	12.30	32.80
		(SD)	(0.188)	(0.173)	(0.886)	(0.212)	(0.293)	(1.180)	(0.736)	(4.620)
		N	25	31	24	28	32	27	15	8
	XIr[3]	Mean	2.66	2.90	7.72	2.73	3.08	8.46	12.90	40.10
		(SD)	(0.177)	(0.284)	(1.120)	(0.184)	(0.232)	(1.100)	(0.664)	(4.480)
		N	52	49	49	133	116	114	108	86
	Grotta dei Fiori SD[4]	Mean	2.32	2.43	5.79	2.25	2.56	5.87	11.10	29.40
		(SD)	(0.427)	(0.386)	(2.080)	(0.215)	(0.302)	(1.280)	(0.901)	(6.690)
		N	9	9	9	16	13	13	8	5
Prolagus sardus	Grotta Teulada[5]	Mean	2.66	3.03	8.05	2.68	2.86	7.75	12.30	35.60
		(SD)	(0.116)	(0.183)	(0.763)	(0.091)	(0.259)	(0.854)	(0.533)	(3.790)
		N	7	6	6	5	4	4	6	4
	VI banco 6[6]	Mean	2.06	2.24	4.62	–	–	–	–	–
		(SD)	(0.134)	(0.177)	(0.591)					
		N	51	48	48	0	0	0	0	0
	Dragonara cave[7]	Mean	2.73	3.05	8.36	2.93	3.24	9.52	13.00	42.40
		(SD)	(0.152)	(0.227)	(0.972)	(0.167)	(0.219)	(1.020)	(0.599)	(4.050)
		N	54	53	53	140	133	132	146	124
	S'Omu e S'Orku[8]	Mean	2.65	2.76	7.48	2.83	3.03	8.58	13.20	40.40
		(SD)	(0.151)	(0.219)	(0.865)	(0.146)	(0.247)	(1.050)	(0.632)	(4.560)
		N	70	71	59	107	64	60	119	56

Ages: [1] latest Pliocene - Early Pleistocene; [2] Middle -?Late Pleistocene; [3] ?Late Pleistocene; [4] Middle Pleistocene (>350 ka); [5] Late Pleistocene; [6] Middle or Late Pleistocene; [7] Late Pleistocene (22,390–21,910 ka cal BP); [8] Holocene.
Variables with a non-normal distribution are underlined, while those without homogeneity of variances among groups are in bold.

Table 4

Femur measurements (in mm) of *P. figaro* and *P. sardus* per fossiliferous site: mean, standard deviation (SD) and number of specimens (N).

			FL	FTDp	FTDd
Prolagus figaro	X3	Mean	50.20	9.37	7.81
		(SD)	(3.020)	(1.090)	(1.330)
		N	2	10	5
	X4	Mean	–	9.55	7.43
		(SD)		(0.746)	(0.484)
		N	0	10	3
Prolagus sardus	Cava Alabastro	Mean	54.10 (–)	9.72	9.70
		(SD)		(1.380)	(0.819)
		N	1	5	3
	XIr	Mean	48.90	10.80	8.59
		(SD)	(2.470)	(0.567)	(0.568)
		N	52	55	58
	Grotta dei Fiori SD	Mean	–	10.10	8.16
		(SD)		(1.180)	(0.850)
		N	0	5	5
	Grotta Teulada	Mean	48.80	10.50	8.84
		(SD)	(2.550)	(0.821)	(0.590)
		N	2	11	8
	VI banco 6	Mean	48.40	10.50	8.48
		(SD)	(2.700)	(0.726)	(0.464)
		N	19	19	19
	Dragonara cave	Mean	50.90	11.20	9.28
		(SD)	(3.180)	(0.944)	(0.724)
		N	39	126	113
	S'Omu e S'Orku	Mean	49.40	10.40	8.70
		(SD)	(2.750)	(0.866)	(0.500)
		N	5	40	39

Variables with a non-normal distribution are underlined, while those without homogeneity of variances among groups are in bold. See ages of fossil sites in Table 2.

Table 5

Tibia measurements (in mm) of *P. figaro* and *P. sardus* per fossiliferous site: mean, standard deviation (SD) and number of specimens (N).

			TL	TAPDp	TTDp	TTDd
Prolagus figaro	X3	Mean	48.50	6.68	6.19	6.25
		(SD)	(2.080)	(0.748)	(0.427)	(0.488)
		N	2	5	5	2
	X4	Mean	–	8.73	8.32	6.99
		(SD)		(0.777)	(0.842)	(0.693)
		N	0	6	6	5
Prolagus sardus	Cava Alabastro	Mean	–	7.42	7.80	6.61
		(SD)		(0.487)	(0.424)	(0.408)
		N	0	5	5	9
	XIr	Mean	53.40	8.76	9.28	7.57
		(SD)	(2.610)	(0.582)	(0.576)	(0.458)
		N	39	36	34	38
	Grotta dei Fiori SD	Mean	–	–	–	6.65
		(SD)				(0.582)
		N	0	0	0	6
	Grotta Teulada	Mean	49.90	7.80	8.20	7.23
		(SD)	(–)	(–)	(–)	(0.403)
		N	1	1	1	6
	VI banco 6	Mean	54.50	8.99	9.71	7.94
		(SD)	(2.500)	(0.478)	(0.271)	(0.576)
		N	9	8	8	9
	Dragonara cave	Mean	56.40	9.35	9.89	8.02
		(SD)	(3.230)	(0.775)	(0.749)	(0.602)
		N	71	124	85	303
	S'Omu e S'Orku	Mean	52.10	8.51	9.15	7.36
		(SD)	(3.250)	(0.709)	(0.769)	(0.588)
		N	4	29	22	16

Variables with a non-normal distribution are underlined, while those without homogeneity of variances among groups are in bold. See ages of fossil sites in Table 2.

Supplementary Data, Appendix A).

Significant correlations were observed among teeth variables, especially when Wm1 was assessed. On the contrary, tooth lengths (Lp3 and Lm1) rarely correlated significantly (Lp3 was only correlated with Wp3 and Wm1; and Lm1 with TRL). The established dependency among teeth variables was mostly isometric ($p < 0.05$, $b = 1$), with the exception of Wm1/Wp3 and TRL/Lm1 (Table 6). By contrast, a general lack of correlation was observed among HL and FL and other postcranial variables. This pattern was also followed by some epiphyses of stylopods (HAPDp and FTDd) (Fig. 3). In the case of distal humerus diameters, they showed a high dependent correlation ($r = 0.952$, $p < 0.05$, $b = 1$). Both variables were also correlated with tibial variables ($r = 0.762–0.943$), although it was only isometric dependent ($p < 0.05$) in the case of HAPDd with TL and TTDd. Regarding FTDp, it was positively correlated with tibial measurements in an isometric way ($r = 0.766–0.895$, $b = 1$) (Fig. 3). Strong and significant correlations ($r = 0.892–1.000$) were also identified assessing tibial variables (Fig. 3, Table 6). In general, they correlated isometrically, excepting TAPDp and TL (hyperallometric) and TTDd and TTDp (hypoallometric). In other words, as tibia increased in length, it became proportionally more robust and tibial head increased at a faster rate than distal epiphysis. Finally, a general lack of significant and dependent relationships was observed among teeth variables and those from postcranium, with few exceptions (Fig. 3, Table 6). Most of them corresponded to Wm1 ($r = 0.786–0.976$), which was isometrically related with femoral and tibial variables ($b = 1$, excepting TTDp $b < 1$). This means that when TTDp and Wm1 increase in size, the latter grow at a lower rate (Table 6).

The first two components yielded by PLSR models were good proxies of morphometric variables (total variance explained = 61,53-99,83%). Notably when Wm1, FTDp, TL, TAPDp and TTDd were considered the dependent variable, the variance explained was over 95%. By contrast, the lower values were obtained when FL and FTDp were assessed (not exceeding 70%). In general, Grotta Teulada and XIr were the fossil sites less correlated with first and second component of PLSR models, contrasting with Dragonara and Cava Alabastro results. The lack of association among populations stated us that they were well differentiated. All morphometric variables were well represented in these two first axes (high explained variances). In this regard, the circle of correlations of the models allowed to identify strong relationships among them. In general, Wm1, FTDp and tibial measurements were disposed together in the same morphospace. This also happened considering: (i) HAPDd and HTDd, and (ii) Lp3 and Wp3. On the contrary, the other variables had more erratic locations. This was particular true in the case of FL, whose correlations were never associated to other traits.

Accordingly to the present results, m1 was the dental element with a higher and significant correlation and dependency with postcranial elements. In the case of long bones, the distal part of the humerus and tibial epiphyses showed the best intercorrelations.

3.3. TSIs and ANCOVA tests

Overall, Sardinian *Prolagus* populations showed TSI_{m1AA} and TSI_{TR-LAA} values >1 considering both ochotonids and leporids as control groups (Table 7). Only in two samples (X4 and Grotta dei Fiori SD), TSI_{m1AA} was <1 when ochotonids were the reference group (0.97 and 0.92 respectively). This means that Sardinian *Prolagus* populations had much larger post-canine teeth (the double or threefold larger) than expected for an average modern leporid of their sizes (ANCOVA test, $p < 0.05$) (Fig. 4; Supplementary Data, Appendix A). When considering ochotonids, these increases were slighter (3%–42% larger) but attestable (ANCOVA test, $p < 0.05$) (Fig. 4; Supplementary Data, Appendix A). Accordingly, the results pointed that Sardinian *Prolagus* was a megalodont lineage when compared to extant ochotonids and leporids.
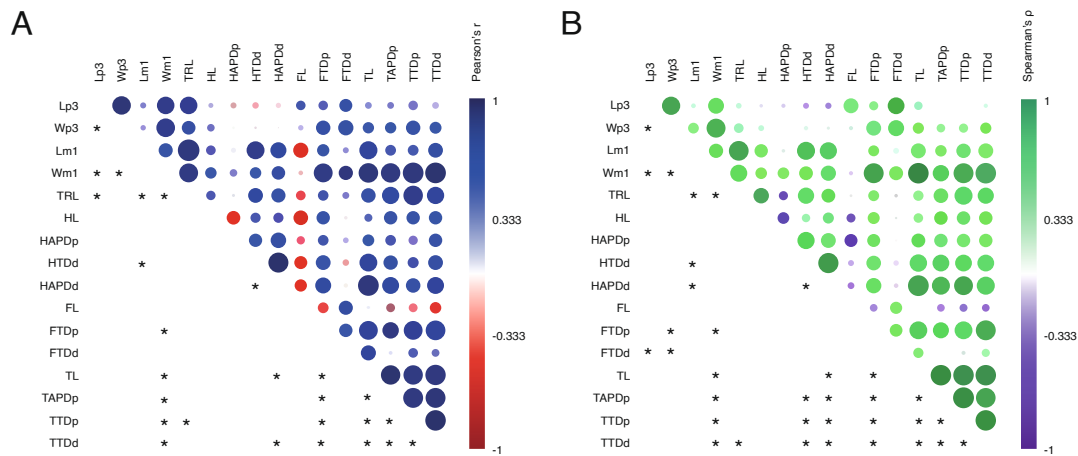
Fig. 3. Pearson's r (A) and Spearman's ρ (B) correlation matrix among variables of teeth, hemimandible and postcranial bones taken on Sardinian *Prolagus*. In the upper triangle, colors and size of circles are indicative of the correlation values, from 1 (blue and green, respectively) to −1 (red and purple). In the lower triangle, asterisks (*) show significant correlations ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 6
Parameters of the linear bivariate regression models ($Y = a + bX$) between teeth and postcranial measurements (which correlated significantly).

Y	X	a	b	p-value	N	r²	RMSE	BIC	VIF	CI b	Scaling
Wp3	Lp3	−0.1	1.299	**<0.001**	9	0.813	0.0289	−31.7	1	0.741–1.857	**b = 1**
Wm1	Lp3	0.103	0.859	**0.009**	8	0.704	0.0212	−32.7	1	0.303–1.414	**b = 1**
Wm1	Wp3	0.24	0.501	**0.007**	8	0.731	0.0202	−33.5	1	0.197–0.805	**b < 1**
TRL	Lm1	0.855	0.575	**0.005**	7	0.823	0.0098	−39.1	1	0.268–0.882	**b < 1**
TRL	Wm1	0.798	0.643	**0.009**	7	0.777	0.011	−37.5	1	0.247–1.040	**b = 1**
Lm1	HTDd	−0.836	1.566	**0.024**	7	0.605	0.0209	−28.5	1	0.306–2.826	**b = 1**
Lm1	HAPDd	0.112	0.343	0.827	5	0.019	0.0395	−13.3	1	−9.17	b = 1
Wp3	FTDp	−1.35	1.75	0.067	9	0.402	0.0516	−21.2	1	−3.808	b = 1
Wm1	FTDp	−0.863	1.304	**0.008**	8	0.718	0.0207	−33.1	1	0.487–2.122	**b = 1**
Lp3	FTDd	−0.272	0.718	0.149	9	0.273	0.0395	−26	1	−2.095	b = 1
Wp3	FTDd	−0.785	1.289	0.058	9	0.424	0.0507	−21.6	1	−2.688	b = 1
Wm1	TL	−2.46	1.7	**0.036**	5	0.816	0.0185	−20.9	1	0.218–3.186	**b = 1**
Wm1	TAPDp	−0.18	0.701	**0.011**	7	0.705	0.0187	−30	1	0.241–1.161	**b = 1**
Wm1	TTDp	−0.088	0.594	**<0.001**	7	0.953	0.0082	−41.5	1	0.441–0.746	**b < 1**
Wm1	TTDd	−0.498	1.119	**<0.001**	8	0.9	0.0124	−41.6	1	0.746–1.493	**b = 1**
TRL	TTDd	0.574	0.608	0.061	7	0.538	0.0158	−32.4	1	−1.3	b = 1
HAPDd	HTDd	−0.458	1.272	**<0.001**	8	0.931	0.0065	−51.9	1	0.927–1.618	**b = 1**
TAPDp	HTDd	−0.355	1.541	0.166	7	0.345	0.0389	−19.7	1	−4.88	b = 1
TTDp	HTDd	−0.314	1.538	0.341	7	0.181	0.06	−13.7	1	−7.52	b = 1
TTDd	HTDd	−0.186	1.293	0.077	8	0.431	0.0278	−28.4	1	−2.97	b = 1
TL	HAPDd	1.153	0.981	**0.016**	6	0.802	0.0099	−33	1	0.304–1.660	**b = 1**
TAPDp	HAPDd	0.104	1.416	0.056	7	0.552	0.0322	−22.4	1	−2.936	b = 1
TTDp	HAPDd	0.025	1.587	0.151	7	0.365	0.0528	−15.5	1	−4.821	b = 1
TTDd	HAPDd	0.204	1.15	**0.025**	8	0.593	0.0236	−31	1	0.198–2.101	**b = 1**
TL	FTDp	0.912	0.792	**0.035**	6	0.712	0.0119	−30.8	1	0.093–1.490	**b = 1**
TAPDp	FTDp	−0.39	1.292	**0.044**	8	0.518	0.0319	−26.2	1	0.047–2.538	**b = 1**
TTDp	FTDp	−1.1	2.01	**0.011**	8	0.636	0.0347	−24.8	1	0.659–3.363	**b = 1**
TTDd	FTDp	−0.419	1.262	**0.002**	9	0.763	0.017	−41.2	1	0.633–1.891	**b = 1**
TAPDp	TL	−2.65	2.07	**0.004**	6	0.901	0.0153	−27.7	1	1.120–3.030	**b > 1**
TTDp	TL	−3.87	2.79	**0.017**	6	0.795	0.0315	−19.1	1	0.824–4.762	**b = 1**
TTDd	TL	−1.69	1.49	**0.009**	6	0.847	0.014	−28.8	1	0.608–2.363	**b = 1**
TTDp	TAPDp	−0.243	1.279	**<0.001**	8	0.898	0.0198	−33.8	1	0.849–1.709	**b = 1**
TTDd	TAPDp	0.219	0.698	**<0.001**	8	0.836	0.0142	−39.1	1	0.390–1.007	**b = 1**
TTDd	TTDp	0.358	0.539	**<0.001**	8	0.908	0.0107	−43.7	1	0.367–0.711	**b < 1**

Columns: *Y* (log-transformed dependent variable), *X* (log-transformed independent variable), *a* (intercept), *b* (slope), *p*-value (of the regression model), N (number of assessed populations), r² (adjusted coefficient of determination), RMSE (root mean square error), BIC (Bayesian information criterion), VIF (Variance Inflation Factor), CI *b* (95% bootstrapped confidence intervals of *b*, N = 1999), Scaling (*b* = 1 indicates isometry, *b* < 1 indicates hypoallometry, and *b* > 1 indicates hyperallometry). Bold type indicates significant *p*-values.

4. Discussion

4.1. Best BM proxy for extinct lagomorphs: A compromise between availability and suitability

Teeth are the most common, sometimes quasi-exclusive remains that palaeontologists can collect from small mammals. In lagomorphs, loose teeth are frequent, whereas complete toothrows (hemimandibles or maxillae) are unusual and postcranial bones are rare (López-Martínez, 1989). In this regard, the taxonomy of most extinct lagomorph species, as well as their body size inferences, have been based on teeth remains. The m1 is historically the preferred tooth for estimating BM in large and

Table 7
TSI_{m1AA} and TSI_{TRLAA} of the different populations of Sardinian *Prolagus* species.

Site	TSI_{m1AA}		TSI_{TRLAA}	
	Ochotonidae	Leporidae	Ochotonidae	Leporidae
X3	1.42	2.97	–	–
X4	0.97	2.06	1.09	1.63
Cava Alabastro	1.12	2.37	1.19	1.75
XIr	1.06	2.26	1.13	1.72
Grotta dei Fiori SD	0.92	1.94	1.03	1.52
Grotta Teulada	1.06	2.25	1.09	1.64
VI banco 6	–	–	–	–
Dragonara cave	1.07	2.28	1.07	1.65
S'Omu e S'Orku	1.13	2.4	1.19	1.8

Values of TSI > 1 indicate megalodontia; whereas values of TSI < 1 mean microdontia.

small extinct mammals (Gingerich et al., 1982; Legendre and Roth, 1988; Legendre, 1989; Damuth and MacFadden, 1990; Millien and Bovy, 2010; Freudenthal and Martín-Suárez, 2013; Moncunill-Solé et al., 2014, 2015, 2016c). However, in lagomorphs, loose m1s are very difficult to identify for non-specialists. Instead, p3 dimensions (the most recognizable tooth at taxonomic level) have traditionally been used to gain a rough idea of the size of extinct lagomorph taxa. Undeniably, the tiny-toothed mainland taxon *Prolagus praevasconiensis* Ringeade, 1979 of the early Miocene of Switzerland, at date the oldest known species of the genus, surely had a smaller BM than the species with the largest p3, the insular taxon *P. imperialis* Mazza, 1987 of the Messinian of Italy (Gargano Peninsula). However, lagomorph researchers suspected that p3/BM scaling relationship was not sufficiently accurate. A preliminary approach for shedding light on this issue was carried out by Moncunill-Solé et al. (2016a), who evidenced different BM scaling patterns in p3 and long bones in some populations of *P. figaro* and *P. sardus*. Paradoxically, *P. figaro* was commonly considered quite larger than its direct descendent *P. sardus* (on the basis of Lp3), but BM estimations based on postcranial bones demonstrated that it was just the opposite (Moncunill-Solé et al., 2016a: Fig. 2).

In accordance with this, the large data set used in the present study revealed a lack of significant correlations between the size of p3 and postcranial bones ($p > 0.05$), demonstrating statistically a decoupling between the size variation of such skeletal remains. A similar disassociation has already been noted in other large and small mammals (Damuth and MacFadden, 1990; Egi, 2001; Millien and Bovy, 2010; Moncunill-Solé et al., 2014, 2015). However, unexpectedly, the study of Sardinian *Prolagus* also established iso- and hypoallometric statistical relationships between m1 (W) and postcranial bones (mainly tibia and femur) ($p < 0.05$; Supplementary Data, Appendix A). In lagomorphs, due to their larger evolutionary variability, p3 and other premolars (upper or lower) are used with taxonomic purposes (López-Martínez, 1989). By contrast, m1 (located in the middle of the toothrow) shows a more conservative morphology and structure (López-Martínez, 1989) and it is not subjected to biting forces, which are concentrated at the front of toothrow (Mazza and Zafonte, 1987). This more "stable" position of m1 could entail a narrower and more persistent scaling trend between its size and BM. As mentioned above, in most lagomorphs, p4 and m1 show a similar overall appearance, what increases the difficulty to distinguish them. However, in the case of *Prolagus*, m1 is characterized by a more curved shaft that may help discriminate it.

Postcranial dimensions (excepting HL, HAPDp, FL and FTDd) were also significantly related ($p < 0.05$, r > 0.762), notably in the case of femur (FTDp) and tibia (TL, TAPDp, TTDp, TTDd) (variation explained >95%, sharing morphospace). This strong scaling relationship is associated to the weight-bearing function that they carry out (Moncunill-Solé et al., 2015). By contrast, teeth experienced more adaptive evolution, and the variation on their size would be related to other biological factors, such as diet (Damuth, 1990). In this regard, skeletal long bones, when available, are preferable as BM proxies in lagomorphs and other

vertebrates. Hindlimb bones are slightly modified by lifestyle in extant ochotonids (Reese et al., 2013), and the sizes of their epiphyses (TAPDp, TTDp, TTDd and FTDp) provided the highest intercorrelation values (Fig. 3). In addition, their growth plates (tibia and femur) count among the last to close in lagomorphs (Geiger et al., 2013), suggesting that they represent better the adult body size. This is well in line with previous studies, which identified these bones as the most suitable BM proxies in lagomorphs (Quintana et al., 2011; Moncunill-Solé et al., 2015, 2016a). Instead, the size variation of some other traits cannot be mainly attributable to a scaling increase/decrease of the body plan (e.g. FL or HAPDp). Several researchers have noted that, in extant ochotonids, the dimensional variation in these latter traits would be more related to their specialized lifestyle, rather than to their BM (Reese et al., 2013; Young et al., 2014). Consequently, they will not be suitable for BM reconstructions of past species. Considering tibia epiphyses, the body masses of *P. figaro* and *P. sardus* were 350 g (ca. 250–460 g) and 500 g (ca. 400–650 g) respectively (Moncunill-Solé et al., 2016a), although significant fluctuations over time were identified.

The scaling relationships among linear dimensional variables (L, W and D) of teeth and long bones belonging to Sardinian *Prolagus* lineage were mainly isometrics (L α D; Table 6). Therefore, our empirical results support both: (i) the geometric similarity approach (L α D α $BM^{1/3}$) (Economos, 1983), and (ii) the Garcia-Silva model (L α D α $BM^{0,37}$) (Garcia and da Silva, 2004, 2006), but disaffirm the ESM (McMahon, 1973, 1975). Moncunill-Solé et al. (2015) established that longitudinal measurements (of long bones and teeth) scale to $BM^{0,36-0,39}$ in ochotonids, with the exception of lengths of long bones (L α $BM^{0,43}$). In this regard, L increases a faster rate than expected by theoretical models. Because the dimensions of bones are strongly depending on limb usage (Garcia and da Silva, 2004, 2006), the particular locomotion of lagomorphs (most of them are very specialized racers and jumpers) probably is key to defining the scaling relationships in this mammalian order. At present and considering the abovementioned, data of extant and extinct lagomorphs likely fit better the Garcia-Silva model.

4.2. Megalodontia: Is it a response to ecological stressors of islands?

Lagomorphs show a dentition perfectly adapted to a fibrous diet (Varga, 2014). The sharpened incisors are used as plant vertical cutters, whereas posterior cheek teeth rows (premolars and molars) grind the food before it is swallowed. The jaw movements are essential for a correct food processing by occlusal surfaces of post-canine teeth, and, ultimately, the food intake should ensure a correct nutrition of the organism (Quesenberry and Carpenter, 2011; Varga, 2014). In this regard, the size (occlusal area or crown height) and shape (pattern of enamel bands and complexity) of cheek teeth are subjected to selection, and their relative values give us clues to the biology and ecology of the species (Lucas, 2004; Famoso et al., 2013).

Sardinian *Prolagus* species showed a significant larger occlusal area of post-canine teeth than extant relatives when size effect was removed (Table 7, Fig. 4). In comparison with leporids, m1AA of these extinct taxa was proportionally much larger (Fig. 4A). Regarding the dental formulae of both groups, leporid lower toothrow includes a bi-lobed m3 (Hillson, 2005), whereas *Prolagus* lacks independent m3 (though having instead a tri-lobed m2). Consequently, the presence of a larger m3 in leporids could entail that each tooth occupies a smaller area (keeping anyway into account that m3 is indeed quite small). On the other hand, the m1AA of Sardinian *Prolagus* was also larger than in extant ochotonids (Table 7, Fig. 4A), but, in this case, both groups have the same lower toothrow pattern (Dawson, 1969; Hillson, 2005). Similarly, when TRLAA was considered, the results also identified a larger post-canine area in Sardinian *Prolagus* (Table 7, Fig. 4B). This latter value is also independent of the number of teeth. Hence, these larger occlusal areas are not solely the result of the size increase that Sardinian ochotonids experienced in insular regimes (Island Rule). Other ecological factors should play a pivotal role in its selection.
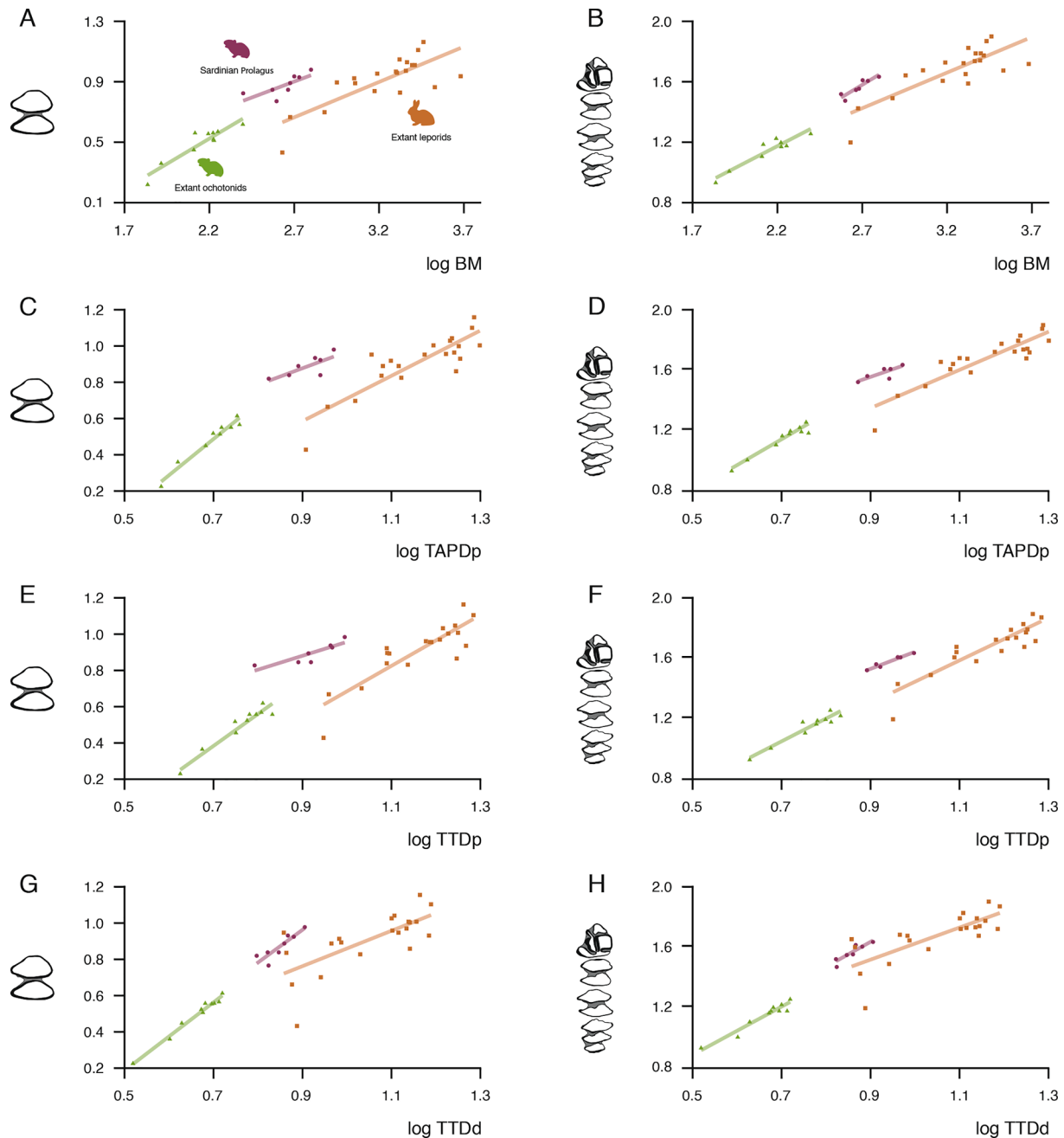
Fig. 4. Bivariate scatterplots between log-transformed body size proxies (BM and tibial epiphyses dimensions) and post-canine areas (A, C, E, G: m1AA; B, D, F, H: TRLAA), considering extant lagomorph species (leporids and ochotonids) and Sardinian *Prolagus*. ANCOVA test identified significant differences ($p < 0.05$) between Sardinian *Prolagus* and extant lagomorphs (ochotonids and leporids), with the exception of panel H where these are only with ochotonid group. Legend: green triangles: extant ochotonids; orange squares: extant leporids; and violet circles: Sardinian *Prolagus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The mastication process evolved to increase the relative surface of food particles, allowing a better action of digestive enzymes and a higher rate of energy acquisition (Lucas, 2004). Thus, evolutionarily, it was established a direct association between rate of energy requirement of mammals and need of mastication. Post-canine teeth (= the masticatory unit) are responsible for food crushing and shearing, and an increase of their occlusal area enhances the chance of food to be fractured at a smaller scale (Lucas, 2004). In mammals, it is stated an evolutionary relationship among cheek tooth size, body size and dietary preferences (considering the extent, stickiness and abrasiveness of food surface) at the specific level (Fortelius, 1985; Lucas, 2004). Whereas the stickiness of food changes during mouthful processing, abrasiveness acts during

the lifespan of the individual, leading even to mastication rate declination consequence of severe wear. In this regard, an increase of occlusal surface of cheek teeth is described as an evolutionary response to a long-term abrasiveness (Lucas et al., 1985; Lucas, 2004).

Lagomorphs are highly selective in food choice, and they usually feed on the most tender and succulent regions of vegetables or plants (buds and young leaves, grasses, or flowers; Quesenberry and Carpenter, 2011). Studying the p3 of insular endemic species of *Prolagus*, Angelone (2005) defined two indices: (i) hypsodonty degree (ibid., Tab. 3, p. 20), which evaluates the absolute value of the tooth shaft height not biased by the overall teeth size; and (ii) density index (ibid., Tab. 1, p. 18), which quantifies the enamel complexity. Two different patterns were

noticed in Sardinian species. *Prolagus figaro* showed an hypsodonty degree similar to congeneric species but a high density index (more complex occlusal surface enamel pattern). On the contrary, *P. sardus* showed the highest, out of scale value of hypsodonty degree among the assessed species (both insular endemics as well as from mainland), but a quite low density index. Both modifications have been noted in small and large herbivores to cope with diet abrasiveness (Jernvall and Fortelius, 2002; Fortelius et al., 2002; Famoso et al., 2013, 2016). In accordance with these results, the diet of past insular endemics is described as more abrasive, as consequence of the limited-resource ecosystems that they inhabited (especially in arid periods) (Alcover et al., 1999; Hautier et al., 2009; Winkler et al., 2013). Frequently, they had to resort to fallback resources and they rooted, overgrazed or near-surface browsed, introducing soil particles (grit) in the ingestion (van der Geer, 2014). In this regard, the sister species from the Gargano palaeo-archipelago (*Prolagus arpicenicus* Mazza, 1987 and *P. imperialis*) have been described as grassland dwellers, well adapted to an abrasive diet (De Giuli et al., 1986). Although at present an in-depth study on the diet of Sardinian *Prolagus* lacks (isotopic or wear analysis), all these evidences suggest a significant feeding shift towards a more abrasive ingestion in Sardinian *Prolagus*. This diet change could have been the evolutionary trigger of megalodontia. Hypsodonty and megalodontia enhance the resistance of tooth wear (Lucas, 2004), whereas an increase of enamel complexity suggests a more efficient food processing but also a lower wear (Pérez-Barberia and Gordon, 1998; Kaiser et al., 2010; Famoso et al., 2013). These eco-evolutionary adaptations maximize the longevity of the permanent dentition and it seems likely that they respond to the same ecological stressors of the insular energy-limited environments.

On the other hand, Angelone (2005) criticized the interpretation that diet shift is the single driver of such dental modifications in insular small-sized endemics (food habits hypothesis), due to the low likelihood that the same type of environment (arid, dry, open ecosystems, with harshly limited resources, and phytolith-rich plants) occurs in all islands. Other biological and ecological factors might have had a main selective role, such as an extended life (life-history hypothesis) (Jordana et al., 2012; Angelone et al., 2017). Some authors have researched the life history of some insular small mammals, and have assessed the relationship of the slow life history with hypselodonty and hypsodonty dental features (Moncunill-Solé et al., 2016b; Angelone et al., 2017). However, the palaeobiological data of the Sardinian *Prolagus* are currently rather limited to draw further conclusions. Also relevant will be assessing cheek teeth size and BM of the coeval mainland congenerics to rule out possible phylogenetic effects, and evaluating the teeth size relative to body mass in the Garganic *Prolagus* to strength the results and conclusions obtained in the present research.

The evolutionary dynamics of teeth size observed here contribute to highlight again the inaccuracy of teeth as size proxy in lagomorphs, because their variations response to shifts in BM but also to ecological stressors (Famoso et al., 2013).

5. Conclusions

Several eco-evolutionary adaptations have been described in fossil insular ochotonids regarding adult body size, teeth features, lifestyle as well as life history. The present paper contributes to this topic testing tooth and long bone scaling, as well as dentition size evolutionary dynamics in the anagenetic lineage of Sardinian *Prolagus* (Early Pleistocene to Holocene). Size variation of p3 is not correlated to other skeletal remains, calling into question the palaeobiological and palaeoecological reconstructions based on it. In fact, m1 was the only teeth item which showed isometric dependent correlations with long bones, attributable to its more conservative position. Long bones, particularly tibia epiphyses, were stated as the most reliable BM proxies in *Prolagus* and probably in extinct lagomorphs.

Sardinian *Prolagus* was identified as a megalodont lineage, whose cheek teeth are significantly larger than those of extant relatives (both

leporids and ochotonids) when the size effect was removed. Besides, Sardininan *Prolagus* dentition is hypsodont (*P. sardus*) and with a more complex enamel pattern (*P. figaro*). Such dental features have been noted in herbivores to face diet abrasiveness, which allow that tooth last for a longer time (food habits hypothesis). In accordance with this and considering the ecology of the studied species, megalodontia may be an evolutionary response to the particular stressors of islands (more abrasive diet). At the moment other biological and ecological factors, such as a longer longevity, cannot be excluded (life history hypothesis).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110645.

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