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First approach of the life history of *Prolagus apricenicus* (Ochotonidae, Lagomorpha) from Terre Rosse sites (Gargano, Italy) using body mass estimation and paleohistological analysis



Première approche sur l'histoire de vie de Prolagus apricenicus (Ochotonidae, Lagomorpha) en provenance de sites des Terre Rosse (Gargano, Italie) par estimation de la masse corporelle et analyse paléohistologique

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ABSTRACT

Research on the biology, especially on life history, of insular endemics is of great importance because they are under specific ecological pressures: low extrinsic mortality and resource limitation. We reconstruct some biological traits of an extinct ochotonid, *Prolagus apricenicus* from Gargano (Late Miocene; Italy). The extinct mainland *Prolagus* cf. *calpensis* is analyzed for comparisons. Our results predict a mass of 350 g for *P.* cf. *calpensis*, 280 for *P. apricenicus* (from Cava Dell'Erba, F1 site), and 600 for *P. apricenicus* (from Cava Fina, F8 site). Though a thorough histological analysis was hampered by the poor preservation of the material, skeletochronology of *P. apricenicus* from F1 indicates a longevity of at least around 7 years for this population. This suggests a slower life history than expected from body size for *P. apricenicus* compared with extant ochotonids.

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R É S U M É

La recherche sur la biologie, spécialement le cycle biologique, des espèces endémiques insulaires est d'une importance capitale, du fait qu'elles sont soumises à des pressions écosystémiques spécifiques : faible taux de mortalité extrinsèque et limitation des

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ressources. Nous avons reconstitué certains caractères de la biologie d'un ochotonidé éteint, *Prolagus apricenicus* de Gargano (Miocène supérieur ; Italie). Le *Prolagus* cf. *calpensis* continental est analysé pour comparaison. Nos résultats prévoient une masse de 350 g pour *P. cf. calpensis*, 280 g pour *P. apricenicus* (de Cava dell'Erba, gisement F1) et 600 g pour *P. apricenicus* (de Cava Fina, gisement F8). Bien que l'analyse paléohistologique complète n'ait pas été possible en raison de la mauvaise qualité du matériel, la squelettochronologie montre pour *P. apricenicus* de F1 une longévité d'environ 7 ans. Ceci suggère une histoire de vie plus lente de ce que laissait prévoir la taille de *P. apricenicus*, par rapport aux ochotonidés vivants.

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1. Introduction

Life history theory underscores the importance of age-specific extrinsic mortality as the mechanistic link between environment and the optimal life history (optimal fitness; Reznick et al., 2002). In this evolutionary context, islands play a relevant role as extraordinary natural laboratories with particular ecological pressures: low extrinsic mortality and resource limitation (MacArthur and Wilson, 1967; Whittaker, 1998). Because life history traits tightly correlate with body mass (Calder III, 1984; Peters, 1983), the size shifts on islands (the Island Rule), observed by Foster (1964) and described by van Valen (1973), are currently the focus of extensive research (Palkovacs, 2003). Nevertheless, little is known about the evolution of life histories in extinct insular mammals. The few studies hitherto done have been focused principally on dwarfing (Bromage et al., 2002; Jordana and Köhler, 2011; Jordana et al., 2012, 2013; Köhler, 2010; Köhler and Moyà-Solà, 2009; Kubo et al., 2011; Marín-Moratalla et al., 2011; Raia and Meiri, 2006; Raia et al., 2003; van der Geer et al., 2014), while the relation between life history evolution and gigantism remains widely neglected.

Lagomorpha (rabbits, hares and pikas) is a mammalian taxon poorly studied in the paleontological field in comparison to other groups such as rodents or taxa of large body size. Most research on fossil lagomorphs has been directed to taxonomical identification or morphology (Angelone, 2007; López-Martínez, 1989) and there have been few studies of their life history. Among the fossil genera of pikas, *Prolagus* Pomel, 1853 (Ochotonidae, Lagomorpha) stands out from the rest for the following reasons. Distributed from Europe to Anatolia during the Cenozoic, it is noticeable for its long paleobiogeographical history of more than 20 million years (López-Martínez, 2001). *Prolagus* probably played an important role in ecosystems as a prey for many species of large and small predators, due to its small size (around half a kilogram) (López-Martínez, 2001).

Prolagus species illustrate the general trend toward a larger body mass in insular ecosystems (Angelone, 2005; López-Martínez, 2001). The size increase in these lagomorphs in comparison with their mainland relatives varies from species to species, but it is attained quickly (Angelone, 2005). In addition, insular *Prolagus* species have a robust skeleton, some complications in premolar morphology, and disproportionate tooth size in relation to their body sizes (Angelone, 2005; López-Martínez, 2001). On

Mediterranean islands, this genus was only present in the Gargano paleoarchipelago and on the Tyrrhenian Islands (Angelone, 2005; López-Martínez, 2001). Particularly, the area of the Gargano paleoarchipelago (Apulia, Italy) was the home of two *Prolagus* species: *Prolagus apricenicus* Mazza, 1987 and *Prolagus imperialis* Mazza, 1987. Both are characterized by significant evolutionary changes in dental morphology and by a marked increase in size (Masini et al., 2010; Mazza, 1987). *Prolagus apricenicus* occurs in all *Terre Rosse* fillings of Late Miocene karst fissures of the Gargano area (Abbazzi et al., 1996). It is smaller and less derived than *P. imperialis*, which is only found in the fissures recording the youngest part of the population history of the Gargano paleoarchipelago (De Giuli et al., 1986, 1990). The paleoisland of Gargano formed part of an archipelago inhabited by a highly unbalanced fauna composed of a large number of rodent species and of remarkable large mammals (hoplitomericids) (Freudenthal, 1976; Masini et al., 2010).

The poor knowledge of the biology of fossil lagomorphs (from islands as well as the mainland) and the absence of studies associated with giant insular mammals and their life history leave open an enormous research field. The distinctive traits of *Prolagus* make it a suitable candidate for assessing the evolution of small mammals on islands. Its history of 20 million years and its great biodiversity (22 species) allow the comparison between mainland and island species of different geological times. Moreover, as *Prolagus* species are prey of mammalian predators on the mainland, the insular species may show clear changes in their life history and body mass as a consequence of the low extrinsic mortality of islands caused by comparatively very low number of carnivores. For this reason, the aim of our research is to reconstruct some biological traits (mass and longevity) of *Prolagus apricenicus* from Gargano and the mainland *Prolagus* cf. *calpensis* Major, 1905 from Casablanca I site (Spain) through regression models and bone histology analyses, respectively. The paleohistological study of long bones allows to reconstruct certain life history traits of extinct mammalian species (Köhler and Moyà-Solà, 2009; Marín-Moratalla et al., 2011). It is difficult to obtain life history traits other than longevity from bone histology of small mammals because the various life stages are completed before the first year and they are thus not recorded in the bone tissue (Castanet et al., 2004; García-Martínez et al., 2011). However, life history traits correlate with body size in a predictable way, allowing inferences about their life history traits using body mass

values (Blueweiss et al., 1978). Finally, the life history strategies observed in extant ochotonas, the closest relatives of *Prolagus*, show two different patterns depending on its habitat (Smith, 1988), allowing additional conjectures about the life history of insular *Prolagus*. Thus, the picture that emerges from these different approaches is a first step towards an understanding of the evolution of life histories and body mass of insular giants.

2. Material and methods

2.1. Material

In this study, we used femora because it is the bone that provides the most accurate age estimations (García-Martínez et al., 2011) and it is a good body mass predictor in lagomorphs (Moncunill-Solé et al., 2015). We selected femora of *P. apricenicus* from two different fissure fillings of the karst network in the Gargano promontory (Italy): Cava Dell'Erba (coded as F1) and Cava Fina (coded as F8) (Table 1). According to biochronology (De Giuli et al., 1986, 1990; Freudenthal, 1976), Cava Dell'Erba site (F1) is older than Cava Fina (F8), though both are dated geologically from the Late Miocene (Freudenthal et al., 2013). Only *Prolagus apricenicus* is described in F1, while in F8 the presence of the second species of *Prolagus* (*Prolagus imperialis*) is not clear (Mazza, 1987). The measures of teeth associated with F8 femora fall within the *P. apricenicus* range (Angelone, 2007). For this reason, we assume that femora from F8 also belong to this species. For comparison, we additionally analyzed remains of the extinct mainland ochotonid *Prolagus* cf. *calpensis* from Casablanca I site (Spain) (Late Pliocene) (Table 1). The remains of *P. apricenicus* belong to the collection of the 1980s field work team led by the late Claudio De Giuli, and are housed at the University of Florence (Italy), while those of *P. cf. calpensis* are housed at the Institut Català de Paleontologia Miquel Crusafont (ICP) (Spain). The thin sections of both species are stored in the collections of the ICP with the acronym IPS.

2.2. Body mass estimation

Adult body size is achieved with skeletal maturation, after growth has strongly decelerated, and is maintained

Table 1

Details of the material of the three *Prolagus* populations used in the study: total number of femora that we have ("Femora" column), number of femora used for the body mass estimation analysis ("Body mass estimation" column) and for the histological analysis ("Histological slides" column).

Tableau 1

Détails des os des trois populations de *Prolagus* utilisés dans l'étude : nombre total de fémurs dont nous disposons (colonne « Fémurs »), nombre de fémurs utilisés pour l'estimation de la masse corporelle (colonne « Estimation de la masse corporelle ») et pour l'analyse histologique (colonne « Coupes histologiques »).

	Femora (n)	Body mass estimate (n)	Histological sections (n)
<i>P. apricenicus</i> F1	43	11	12
<i>P. apricenicus</i> F8	24	24	17
<i>P. cf. calpensis</i>	10	5	6

until the animal dies (Peters, 1983). We estimated mass only on postcranial sample of individuals that had already attained skeletal maturity, as shown by fused epiphyses (Table 1). We did not take measurements or estimate body mass in specimens with unfused or broken epiphyses. Also, we did not assume body mass differences between sexes in extinct ochotonids because sexual dimorphism of extant *Ochotona* Link, 1795 is minimal (Nowak, 1999; Smith, 1988).

Femoral measurements were used to estimate the body mass of the three populations of *Prolagus* following the criteria of Moncunill-Solé et al. (2015). The antero-posterior and transverse diameters of the epiphyses of femora, as well as their lengths, are good body mass predictors in the order Lagomorpha ($r^2 > 0.954$, $SEE < 0.12$). The following measurements were taken on *Prolagus* remains with a digital caliper (0,05 mm error): femoral length (FL), proximal femoral transversal diameter (FTDp), distal femoral antero-posterior diameter (FAPDd) and distal femoral transversal diameter (FTDd). We used bivariate regressions between these measurements and body mass to predict the weight of extinct *Prolagus* (for equations see Table 2).

2.3. Paleohistology

For obtaining the histological sections, we selected an ontogenetic series of specimens, from juveniles to adults (Table 1), and followed the criteria for rodents described by García-Martínez et al. (2011). The femora were embedded in epoxy resin (Araldite 2020) and, later, the surface of interest (central part of the diaphyses, below the third trochanter) was exposed with a Buehler Isomet low speed saw. The surface was polished on a glass sheet coated with carborundum powder with decreasing particle size (from 600 up to 1000 grit). We fixed the resin block to a frosted glass slide using ultraviolet curing glue (Loctite 358). The thin sections were prepared with a diamond saw (Buehler, PetroThin) to a final thickness of about 100–120 μm . Thin sections were polished with a gradient of carborundum (800 and 1200 grit) and dehydrated through a graded series of alcohol baths, cleared in Histo-Clear II during five minutes and finally mounted in DPX mounting medium. Slices were examined under linearly and/or circularly polarized light without or with a 1 λ filter (Zeiss Axio-Scope A1, Zeiss AxioCam ICc5; and Leica DM 2500 P, Leica DFC 490).

For histological analysis, the bone tissues are described following the classification of de Margerie et al. (2002) and de Ricqlès et al. (1991). Bone tissue may contain lines of arrested growth (LAGs) indicating periods of arrested osteogenesis (Chinsamy-Turan, 2005). LAGs are ubiquitous in mammals and record annual cycles of growth, metabolic rate and hormone levels (Köhler et al., 2012). When the growth rate suddenly decreases at maturity, we can distinguish the External Fundamental System (EFS), a highly organized lamellar bone with the presence of LAGs that makes up the outer cortex. The number of LAGs throughout the whole primary bone represents the age at death of the specimen (Castanet, 2006; Erickson, 2005; Marín-Moratalla et al., 2011, 2013). The tissue representing

Table 2

Body mass estimates (in grams) for the three *Prolagus* populations: mean, the confidence interval (in brackets), the sample size of fossil individuals (*n*), and the weighted mean (MEAN) calculated from all estimates. The measurement used in each row is indicated in the first column (FL: femoral length; FTDp: proximal femoral transversal diameter; FAPDd: distal femoral antero-posterior diameter; FTDD: distal femoral transversal diameter).

Tableau 2

Estimations de la masse corporelle (en grammes) des trois populations de *Prolagus*: moyenne, intervalle de confiance (entre parenthèses), taille par échantillon d'individus fossiles (*n*), et moyenne arithmétique pondérée (MEAN), calculée à l'aide des différentes mesures. La mesure utilisée dans chaque ligne est indiquée dans la première colonne (FL: longueur du fémur; FTDp: diamètre transversal de l'épiphyse proximale du fémur; FAPDd: diamètre antéro-postérieur du fémur distal; FTDD: diamètre transversal du fémur distal).

	<i>P. apricenicus</i> F1		<i>P. apricenicus</i> F8		<i>P. cf. calpensis</i>	
FL	269.47	<i>n</i> = 3	–	–	–	–
(logBM = $-1.11 + 2.229\log\text{FL}$)	(249.26–289.68)					
FTDp	313.84	<i>n</i> = 11	658.80	<i>n</i> = 14	369.32	<i>n</i> = 4
(logBM = $0.498 + 2.217\log\text{FTDp}$)	(262.45–365.22)		(612.86–704.73)		(312.00–426.64)	
FTDd	235.83	<i>n</i> = 6	553.92	<i>n</i> = 9	300.51	<i>n</i> = 1
(logBM = $0.318 + 2.481\log\text{FTDd}$)	(216.90–254.76)		(505.49–602.35)			
FAPDd	276.64	<i>n</i> = 6	590.26	<i>n</i> = 10	403.69	<i>n</i> = 1
(logBM = $0.225 + 2.63\log\text{FAPDd}$)	(255.71–297.58)		(549.05–631.46)			
MEAN	282.13		609.43		363.58	
	(225.89–328.16)		(510.42–704.10)		(268.59–469.59)	

a given ontogenetic stage, however, results from different morphogenetic processes such as remodeling, differential growth rates or drift (Castanet, 2006), or even growth arrest in bone thickness (Castanet et al., 2004). Therefore, the age obtained through skeletocronological analysis always represents the minimum age at death of an individual.

2.4. Extant species of ochotonas data (*Ochotona princeps* and *Ochotona curzoniae*)

Ochotona (pikas) is the phylogenetically closest relative of *Prolagus*, because the leporid–ochotonid dichotomy occurred in the Oligocene (Smith, 2008). Extant pikas show two different life history strategies related to different ecosystems: rocky versus meadow habitat. Meadow-dwelling pikas have a faster life history strategy than rock-dwelling species (Smith, 1988). For comparison with extinct *Prolagus*, we selected one species from each habitat (*Ochotona princeps* Richardson, 1828 and *Ochotona curzoniae* Hodgson, 1857) and searched the literature about their body mass and life history traits. These traits can contain phylogenetic information (taxa that are closely related, in this case all *Ochotona* species, in general are more similar to each other than remotely related taxa, *Prolagus* species) (Laurin et al., 2004). For this reason, the comparisons with extant ochotonas have to be made cautiously (shifts in life history traits, see below).

2.5. Life history traits predicted by body mass

The allometric models described in the literature for mammals (Blueweiss et al., 1978; Cabana et al., 1982; Millar, 1977; Millar and Zammuto, 1983) (for equations see Table 3) allow estimation of life history traits (longevity, age at sexual maturity, age at weaning, litter size, number of litters and mass at birth) from the body mass of the species (estimations in the case of the three populations of *Prolagus* or observed values in the case of extant ochotonas) and provide an allometric context for our results. However, the prediction of life history traits using body mass values is not always reliable. As a consequence of the selective regime of the environment, as is the case of islands, many

species live far longer and mature faster (or more slowly) than expected from their body mass (Stearns, 1992).

3. Results

3.1. Body mass estimation for *Prolagus* species

The body mass estimations for the three populations of *Prolagus* are shown in Table 2. The sample sizes for the body mass estimation of the three populations are very different, but the fragmentation of bones and the unfused epiphyses do not allow a larger sample size. *Prolagus apricenicus* of the older fissure (F1) weighed around 280 g, and the different measurements predict estimations ranging from 235.83 to 313.84 g. In F8, we estimated a mass around 610 g and the different predictions range from 553.92 g to 658.80. In the case of *Prolagus* from Casablanca, we estimated a body mass around 360 g, ranging from 300 to 400 g.

3.2. Paleohistology

In fossil remains, a good preservation of bone tissues is indispensable to obtain suitable thin sections. In our case, most *Prolagus* femora show microbial/fungal attack or are slightly splintered (especially in *P. cf. calpensis* and *P. apricenicus* F8) (Fig. 1A, B). This poor state of preservation complicates determination of the tissue type and of the presence and number of LAGs, thus reducing the size of the already small available sample. This is especially the case in *P. cf. calpensis*, where the microbial/fungal attack hampers thorough analysis, which made the interpretation and description of bone tissue impossible (Fig. 1A).

3.2.1. *Prolagus apricenicus* from Cava Dell'Erba F1

The femoral thin sections show an appropriate degree of preservation of bone tissue, allowing a full histological study of this species. The small femora with unfused epiphyses show a juvenile ontogenetic stage consisting of a fast-growing fibrolamellar complex (FLC) with both simple vascular canals and longitudinal primary osteons (Fig. 2A, B). On the medial side of the cortex, a strong muscular insertion area is revealed by the presence of Sharpey's fibres.

Table 3

Life history information for extinct *Prolagus* analyzed here and two extant species of *Ochotona* (*O. princeps* and *O. curzoniae*). Adult mass of *Prolagus* are the inferred values, and of *Ochotona* are from the literature (see references in the text). Life history traits (longevity, sexual maturity age, weaning age, litter size, no. of litters and mass at birth) are estimated with the adult mass (AM, second row) (see references in the text) or are those observed/inferred (obtained from the literature in ochotonas, see references in the text; or inferred from paleohistological data in *Prolagus*). Values with asterisk are merely inferences of the values of the life history traits estimated through body mass (see the text). In ochotonas, the differences between the observed values (literature) of life history traits and those predicted from their body masses are marked with different symbols: =: when the predicted and observed value coincide; <: when the observed value is lower than the predicted; >: when the observed value is greater than the predicted.

Tableau 3

Information sur l'histoire de la vie des *Prolagus* éteints analysés et de deux espèces actuelles d'*Ochotona* (*O. princeps* et *O. curzoniae*). Les masses corporelles des *Prolagus* adultes sont les valeurs inférées et, dans le cas d'*Ochotona*, les masses proviennent de la littérature (voir les références dans le texte). Les caractéristiques de l'histoire de vie (comme la longévité, l'âge de la maturité sexuelle, l'âge du sevrage, la taille des portées, le nombre de portées et la masse à la naissance) sont estimées à partir de la masse des adultes (AM, deuxième rangée) (voir les références dans le texte) ou sont celles observées/inférées (obtenues à partir de la littérature pour *Ochotona*, voir les références dans le texte ; ou inférées à partir de données paléohistologiques de *Prolagus*). Les valeurs avec astérisque sont des estimations sur les valeurs des caractéristiques d'histoire de vie, fondées sur la masse corporelle (voir le texte). Dans les cas d'ochotonas, les différences entre les valeurs observées (littérature) des traits de l'histoire de vie et celles prédites à partir des masses corporelles sont marquées par divers symboles : =, lorsque les valeurs prédites et observées coïncident ; <, lorsque la valeur observée est inférieure à celle qui est prédite ; >, lorsque la valeur observée est supérieure à celle qui est prédite.

	<i>P. apricenicus</i> F1	<i>P. apricenicus</i> F8	<i>P. cf. calpensis</i>	<i>O. princeps</i>		<i>O. curzoniae</i>	
Common name	–	–	–	North American pika		Black-lipped pika	
Habitat	–	–	–	Talus and rockpiles		Meadow	
Adult body Mass (AM)	282.13 g	609.43 g	363.58 g	169.50 g		131.48 g	
Longevity (wild)							
Estimated by AM (Longevity = 630AM ^{0.17})	4.50 years (4.34–4.62)	5.13 years (4.99–5.26)	4.70 years (4.47–4.91)	4.13 years	>	3.96 years	<
Observed/Inferred	6–7 years	? >3 years	?	6 years		1–2 years	
Sexual maturity age							
Estimated by AM (Age Maturity = 0.92AM ^{0.27})	237 days* (224.72–248.56)	292 days* (280.04–305.45)	256 days* (235.47–273.81)	208 days	>	194.17 days	=
Observed/Inferred	–	–	–	347 days		During 1st year	
Weaning age							
Estimated by AM (Weaning Age = 19.56AM ^{0.05})	25.94 days* (25.65–26.13)	26.95 days* (26.72–27.15)	26.27 days* (25.87–26.60)	25.28 days	=	24.96 days	<
Observed/Inferred	–	–	–	3–4 weeks		18 days	
Litter size/No. of litters							
Estimated by AM (Litter Size = 3.43AM ^{-0.16})	4.19 offspring* (4.10–4.35)	3.71 offspring* (3.63–3.82)	4.03 offspring* (3.87–4.23)	4.55 offspring	<	4.75 offspring	=
Observed/Inferred	–	–	–	3 offspring/2 litters		3–6 offspring/3 litters	
Weight at birth							
Estimated by AM (Weight Birth = 0.061AM ^{0.94})	12.28 g* (9.95–14.14)	25.30 g* (21.42–28.98)	15.57 g* (11.71–19.80)	11.50 g	=	–	–
Observed/Inferred	–	–	–	10–12 g		–	

During ontogeny, the FLC is progressively resorbed internally around the medullary cavity while an inner cortical layer (ICL) of new lamellar endosteal bone is deposited and the periosteal apposition of poorly-vascularised (simple longitudinal vascular canals) parallel-fibered bone (PFB) increases the bone diameter. In the anterior region of the cortex, juvenile FLC bone is sandwiched between the ICL and the PFB (Fig. 2C). A clear cementing line (periosteal resorption) marks the transition from FLC to PFB. This line is not considered a LAG and consequently we do not take it into account for calculating longevity. However, in the lateral region of the cortex the tissue transition is more gradual, without the presence of a resorption line, and the PFB is more vascularised than in the anterior region (Fig. 2D). The PFB tissue fills the complete cortex of the posterior region and the outermost cortex of the anterior and lateral regions. The muscular insertion area with Sharpey's fibers at the medial side is present during all ontogenetic stages.

Later in ontogeny, most of the cortex consists of PFB, and Haversian systems (HS) are intruding from the medullary cavity into the innermost cortex. Additionally, an external fundamental system (EFS) is deposited on the outer cortex (Fig. 2E). There is a higher apposition rate of the EFS in the lateral region of the cortex, where several widely-spaced LAGs are present (Fig. 2F). IPS-83891 is the oldest individual of our sample; it shows 7 LAGs in the EFS, suggesting a minimal age of 7 years for this specimen (Fig. 2G). The bone forming process at the lateral region of the cortex modifies the cross-sectional shape and increases the lateromedial length at midshaft. These later ontogenetic changes in bone tissue occur in individuals with fused epiphyses.

Although there is a clear relation between the histological ontogenetic stage, the size (midshaft diameters) and the skeletal maturity (fused or unfused epiphyses), some individuals do not follow this pattern (Table 4). IPS-83892 is an unfused femur showing an early juvenile ontogenetic stage, but has a large antero-posterior diameter at midshaft. This

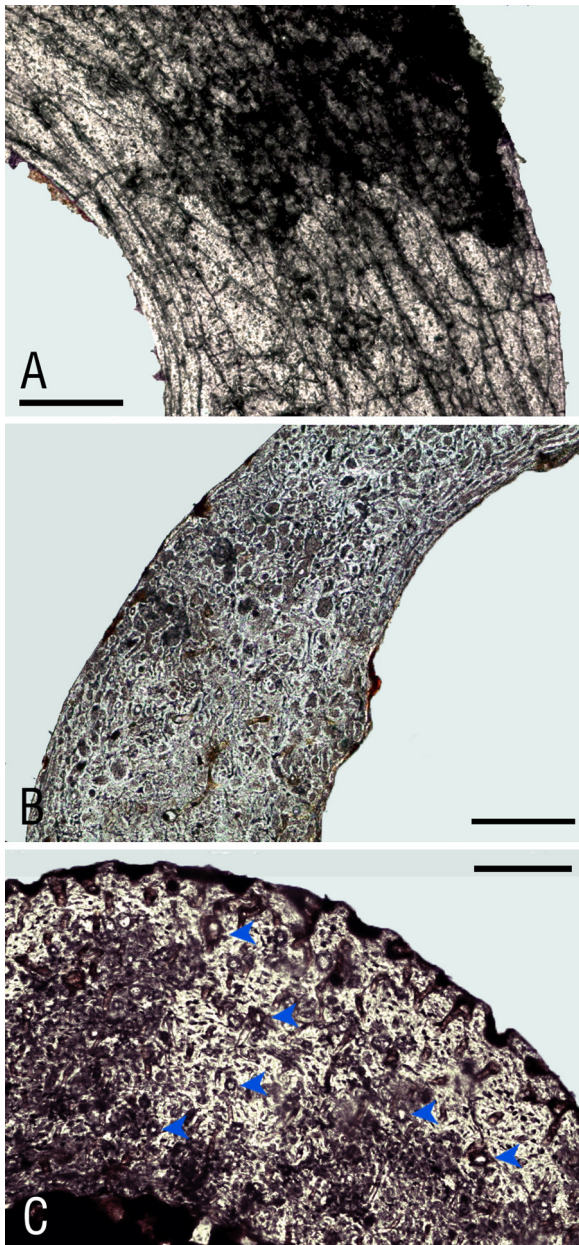


Fig. 1. (Color online.) A. Bone histology of *P. cf. calpensis* from Casablanca I (IPS-81937). The bad preservation and microbial attack can be observed. B and C. Bone histology of *P. aprigenicus* from Cava Fina F8. B shows the bad preservation (IPS-83559) and C the highly vascularised periosteal bone (IPS-83158). Primary osteons are indicated with blue arrowheads. Scale bar: 200 μm (without filter).

Fig. 1. (Couleur en ligne.) A. Histologie osseuse de *P. cf. calpensis* de Casablanca I (IPS-81937). La mauvaise conservation et l'attaque microbienne peuvent être observées. B et C. Histologie osseuse de *P. aprigenicus* de Cava Fina F8. B montre la mauvaise conservation (IPS-83559) et C la forte vascularisation du périoste (IPS-83158). Des ostéons primaires sont indiquées par des pointes de flèche bleues. Échelle : 200 μm (sans filtre).

could reflect size fluctuations or gradual size increase in time of the species (Alcover et al., 1981; van der Geer et al., 2013). On the other hand, the transverse midshaft diameter of this juvenile individual is among the smallest. This is consistent with the fact that this diameter is highly

Table 4

Morphological data on the femora used in the paleohistological analysis. Indicated are the specimen number, APD (antero-posterior diameter at the midshaft, in mm), TD (transversal diameter at the midshaft, in mm) and the epiphysis fusion (U: unfused; F: fused; B: broken; PF/DU: proximal fused and distal unfused; PF: proximal fused; DSL: distal with suture lines).

Tableau 4

Données morphologiques sur les fémurs utilisés dans l'analyse paléohistologique. Sont indiqués : le numéro du spécimen, APD (diamètre antéro-postérieur diaphysaire, en mm), TD (diamètre transversal diaphysaire, en mm) et la fusion de l'épiphyse (U : non fusionnée ; F : fusionnée ; B : brisée ; PF/DU : proximale fusionnée et distale non fusionnée ; PF : proximale fusionnée ; DSL : distale, avec lignes de suture).

Specimen	APD (mm)	TD (mm)	Epiphysis fusion
<i>Prolagus aprigenicus</i> from Cava Dell'Erba F1			
IPS-83885	2.72	3.37	F
IPS-83886	2.88	3.74	F
IPS-83887	2.80	3.62	F
IPS-83888	2.84	3.51	PF/DU
IPS-83889	2.89	3.37	U
IPS-83890	2.87	3.64	U
IPS-83891	2.94	3.45	B
IPS-83892	2.97	3.12	U
IPS-83893	2.86	3.34	U
IPS-83894	2.34	2.73	U
IPS-83895	2.41	2.93	U
IPS-83896	2.28	2.60	U
<i>Prolagus aprigenicus</i> from Cava Fina F8			
IPS-83156	4.35	5.26	U
IPS-83157	3.21	4.08	U
IPS-83158	3.33	3.56	U
IPS-83159	4.36	5.98	U
IPS-83160	3.53	4.02	U
IPS-83161	3.66	4.49	U
IPS-83162	3.65	4.38	U
IPS-83163	3.06	3.81	U
IPS-83559	2.21	3.01	U
IPS-83560	2.96	3.86	U
IPS-83561	4.30	5.35	U
IPS-83562	4.22	5.65	U
IPS-83563	3.38	3.93	U
IPS-83564	3.84	4.86	U
IPS-83565	3.84	4.75	U
IPS-83566	4.25	5.11	PF
IPS-83567	4.50	5.28	DSL
<i>Prolagus cf. calpensis</i>			
IPS-81937	2.66	3.66	PF
IPS-83568	2.64	3.52	U
IPS-83569	3.19	4.07	U
IPS-83570	3.23	4.05	U
IPS-83571	2.78	3.89	U
IPS-83572	2.57	3.29	U

modified during adult stage by apposition of lamellar bone (EFS) on the lateral side, but this also reflects shape variability.

3.2.2. *Prolagus aprigenicus* from Cava Fina F8

Some of the *P. aprigenicus* femora from F8 show microbial/fungal attack and their internal bone structures are largely destroyed and fractured. Consequently, both the skeletochronological analysis and the histological interpretations are ambivalent. The observed traits, however, suggest a similar ontogenetic pattern as in *P. aprigenicus* from F1.

The smallest individuals present a fast-growing FLC with primary osteons and some longitudinal simple vascular canals (Fig. 1C). Furthermore, as in *P. aprigenicus* from

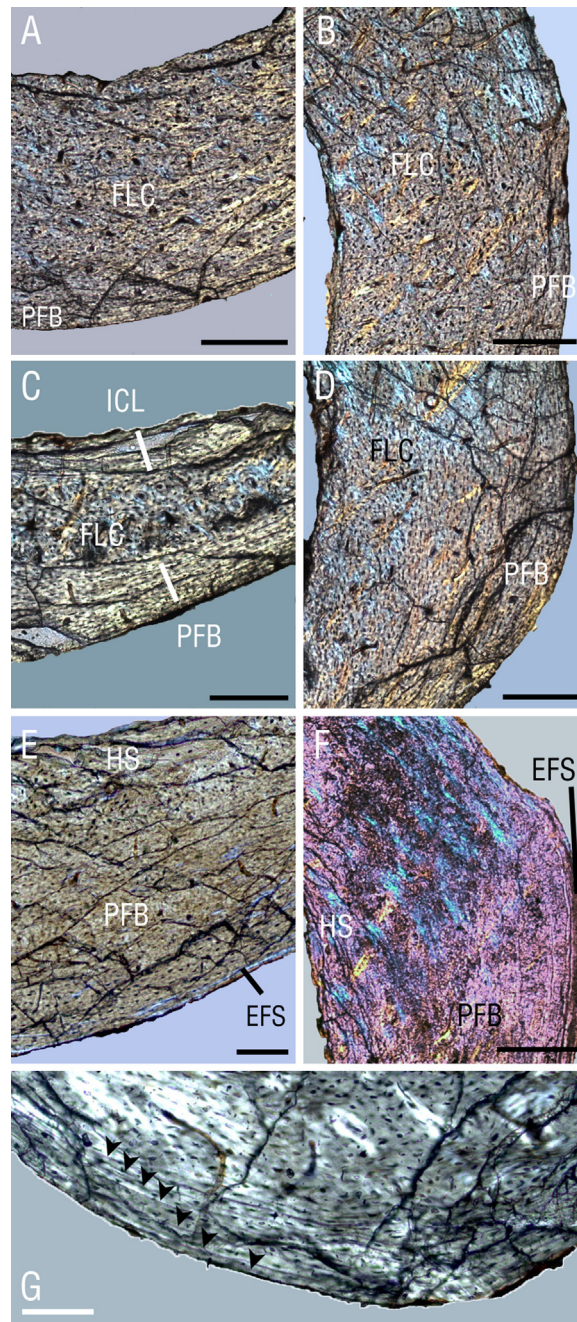


Fig. 2. (Color online.) Bone histology of *P. apricenicus* from Cava Dell'Erba F1 fissure filling. A and B. Anterior and lateral regions of IPS-83892 respectively, a young specimen. It shows the fibrolamellar complex (FLC). C and D. Anterior and lateral regions of IPS-83893 respectively, a mature specimen, showing the fibrolamellar complex (FLC) being resorbed and replaced by the inner cortical layer (ICL) and a parallel-fibered bone (PFB). E and F. Anterior of IPS-83887 and lateral regions of IPS-83886 respectively, old specimens, showing a parallel-fibered bone (PFB) with the external fundamental system (EFS). Haversian Systems are observed (HS). LAGs can be observed in the EFS. G. Detail of the EFS in the lateral region of IPS-83891 with the presence of LAGs (arrowheads). Scale bar of A–F: 200 μm (with 1 λ filter) and of G: 100 μm (without filter).

Fig. 2. (Couleur en ligne.) Histologie osseuse de *P. apricenicus* de Cava Dell'Erba, gisement F1. A et B. Zones antérieure et latérale de IPS-83892, respectivement, jeune spécimen, montrant le complexe fibrolamellaire (FLC). C et D. Zones antérieure et latérale de IPS-83893, respectivement, spécimen adulte, montrant le complexe fibrolamellaire (FLC) résorbé et remplacé par la couche interne du cortex (ICL) et un os à fibres parallèles (PFB). E et F. Zones antérieure de IPS-83887 et latérale de IPS-83886, respectivement, spécimens âgés, montrant un os à fibres parallèles (PFB) avec le système fondamental externe (EFS). Des systèmes de Havers (HS) sont observés. Des lignes d'arrêt de croissance (LAGs) peuvent être observées dans l'EFS. G. Détail de l'EFS dans la zone latérale de IPS-83891, avec présence de LAGs (pointes de flèches). Barre d'échelle de A–F : 200 μm (avec filtre 1 λ) et de G : 100 μm (sans filtre).

Cava Dell'Erba F1, these femora exhibit Sharpey's fibers on the medial side of the cortex for muscle attachment. Later in ontogeny, individuals with good preservation of bone tissue show a FLC tissue in the inner region of the cortex and a PFB tissue in the outer cortex. The older specimens also show endosteal bone (ICL) and an EFS with several LAGs, though the poor preservation of the tissue does not allow counting the number of them.

3.3. Life history traits predicted from body mass estimations of extinct *Prolagus* and extant *Ochotonas*

The body mass estimations of the three populations of *Prolagus* allow prediction of some life history traits for these species. The results of life history traits predictions through body mass are in Table 3 ("Estimated by AW" rows). As a consequence of their larger size, *P. apricenicus* from F8 show values of longevity, sexual maturity age, weaning age and mass at birth greater than *P. apricenicus* F1 and *P. cf. calpensis*, while the latter are expected to have greater litter size. Comparing observed values with those expected from body mass in extant *Ochotonas*, it is noticed that *O. princeps* has a higher longevity and greater age at sexual maturity than predicted from body mass, while *O. curzoniae* shows the opposite pattern (smaller values).

4. Discussion

In extinct taxa, biological variables such as body mass or life history traits cannot be observed directly. Body size (body mass) is of particular relevance because of its implication for the fitness of individuals (Blanckenhorn, 2000) and because of its strong correlation with physiological and life history traits (Calder III, 1984; Peters, 1983; Roff, 1992; Stearns, 1992). This is one of the first studies that addresses the biology (life history traits) of extinct lagomorph species through two analyses: body mass estimation and paleohistology (Riyahi et al., 2011).

The two species of *Prolagus* show body masses intermediate between extant *Ochotona* (pikas) and Leporidae (rabbits and hares) (Fig. 3), slightly overlapping with smaller leporids (*B. idahoensis* and *R. diazi*) but larger than any extant pika. *Prolagus cf. calpensis* weighed around 350 g, a value that is in accordance with previous estimates (Moncunill-Solé et al., 2015). The mean body mass of *P. apricenicus* specimens from the older fissure filling F1 is around 280 g, whereas specimens from the slightly younger F8 have a mean body mass of 600 g. This important body size shift is also observed in tooth size (Mazza, 1987). The insular (hence, expected giant) F1 population shows a lower body mass than the mainland *P. cf. calpensis* (*t*-student, $P < 0.05$) (Table 2). It is widely accepted that small insular mammals tend to become giants with respect to the size of their mainland ancestors (Foster, 1964; Lomolino, 2005). In this case, *Prolagus oeningensis* König, 1825, considered the mainland ancestor of the pikas from Gargano, is of smaller size when teeth are analyzed (Angelone, 2005). Thus, both populations of *P. apricenicus* can be considered as giants. Moreover, although the body size shift is considered a fast process, we do not know the time span during which the F1 population was isolated under the different

selective regime of the insular ecosystem. All fissures of *Terre Rosse* are referred chronologically to the Late Miocene (Freudenthal et al., 2013) and the moment when the ancestral species settled on the island is unclear. It is not known whether *P. apricenicus* of younger fissures (F8) had attained the final (giant) size or whether it is an intermediate form between older fissures as F1 and much younger fissures such as San Giovannino or F32.

The analysis of bone tissue is used to observe differences in growth patterns and life histories. Unfortunately, the poor preservation of the bone tissue of *P. cf. calpensis* hampers the comparison between mainland and insular *Prolagus* species. The histological analysis of *P. apricenicus* provides evidence of deposition of two primary bone tissue types before deposition of the EFS. The juvenile ontogenetic stage presents only a FLC, followed by a slower-growing bone tissue (PFB). Only the specimens with fused epiphyses show a clear EFS with several LAGs. A minimum longevity of 7 years is estimated for this species, based on the number of LAGs in the EFS of IPS-83891. The appearance of the EFS is likely related to skeletal maturity (Horner et al., 2009).

As mentioned above, extant pikas show two different life history strategies related to different ecosystems: rocky or meadow habitat (Smith, 1988). The two species selected for comparisons with *Prolagus* show clearly different life histories. The rock-dwelling American pika (*Ochotona princeps*) weighs 169.5 g (mean). It produces a litter of 2 to 4 young in 30 days and weans around the 3rd or 4th months after birth. Moderately well-camouflaged in their natural habitat (Svendsen, 1979), they are preyed upon by coyotes, longtail and shorttail weasels and pine martens, and can attain a maximum age of 7 years (Silva and Downing, 1995; Smith and Weston, 1990). On the other hand, the plateau pika (*Ochotona curzoniae*) weighs 131.48 g (mean). It has about 4 to 5 young per litter, a gestation period of 20 days and weaning at the 21st day after birth. Their lifespan in the wild is 1 or 2 years, and they are preyed upon by a series of birds of prey (*Falco tinnunculus*, *Mulvus lineatus*, *Buteo hemilasius*, *Corvus corax*), weasels and polecats (*Mustela*) (Qu et al., 2013; Schaller, 1998; Smith et al., 2003). This information and the life history traits of *Ochotona* and *Prolagus* species expected from body mass are summarized in Table 3. Comparing observed (wild) and modeled (from their body mass) life history trait values of extant pikas, *Ochotona princeps* shows a higher longevity, a later age at sexual maturity and a smaller litter size than expected from body mass (Table 3). In contrast, *O. curzoniae* has a shorter life span and a shorter weaning age for its mass (Table 3). Lifespan varies with body size of the species, but the correlation is not perfect. The principal confounding factor is the level of extrinsic mortality (Healy et al., 2014; Stearns, 1992). In addition, the two ecotypes of pikas show differences in their levels of mortality. Rock-dwelling species have a low average yearly mortality while a high annual mortality is observed in meadow species (Smith, 1988). The optimal camouflage of the prey and the difficulty of hunting in the rocky habitat may play an important role in reducing the extrinsic mortality of the long-lived pikas. Consequently, rock-dwelling species of *Ochotona* show a slower life history (longer time to maturity) than

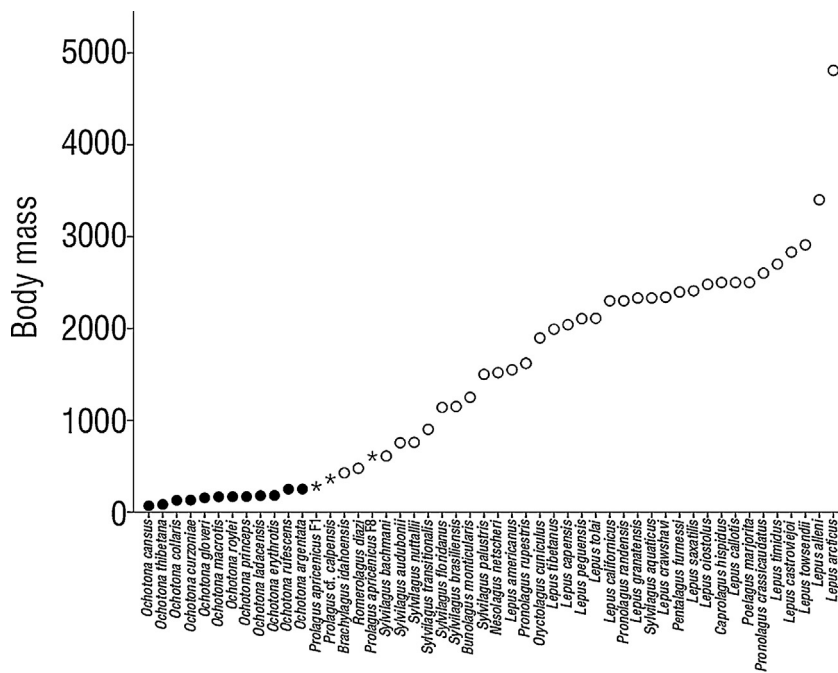


Fig. 3. Representation of the adult body mass (mean) variability of the extant species of lagomorphs and the values obtained in our estimations for *Prolagus* species. Black circles represent the genus *Ochotona*, white circles, leporids, and *Prolagus* species are represented by asterisks. Values for body masses of extant species are taken from Moncunill-Solé et al. (2015).

Fig. 3. Représentation de la variabilité de la masse corporelle des adultes (moyenne) des espèces de lagomorphes vivantes et valeurs estimées pour les espèces de *Prolagus*. Les cercles noirs représentent le genre *Ochotona*, les cercles blancs, les léporidés et les espèces de *Prolagus* sont représentées par des astérisques. Valeurs de masse corporelle des espèces vivantes, d'après Moncunill-Solé et al. (2015).

expected for their size, while meadow-dwelling pikas live faster.

Prolagus apricenicus dwelled in an insular ecosystem characterized by low presence of mammalian predators (only represented by the marine otter *Paralutra garganensis*) and, thus, a low extrinsic mortality (Masini et al., 2010; Sondaar, 1977). Analyzing its life history traits, the estimated longevity of population F1 of *P. apricenicus* using skeletochronology is higher than expected given its body mass (Table 3). This pattern is similar to that observed in rock-dwelling pikas, despite its smaller size. Unfortunately, the longevity estimates of the F8 population are not coherent enough to make strong inferences about its lifespan. Considering the longevity of ochotonas, *Prolagus apricenicus* F1 might present a slower life history than *Prolagus* species that dwell in high-predation habitats (essentially mainland species) due to the differences in the levels of extrinsic mortality. Furthermore, following the pattern of life history traits observed in extant pikas, we suggest for *P. apricenicus* a later age at maturity and a smaller litter size than expected given its size (Table 3). Although we cannot analyze the paleohistology of *P. cf. calpensis*, the high-predation mainland habitat where it lived (Soto and Morales, 1985) suggests a faster life history than that of *P. apricenicus*.

5. Conclusions

To sum up, our study provides an estimated mass of 350 g for *P. cf. calpensis*, 280 g for *P. apricenicus* F1 and 600 g

for *P. apricenicus* F8, values that are intermediate between the body mass ranges of extant pikas and leporids. Skeletochronological analysis suggests an extended longevity for *Prolagus apricenicus* F1 (7 years). Currently, two ecotypes of pikas are described with different life history strategies as a consequence of different levels of extrinsic mortality. Rock-dwelling species under lower extrinsic mortality levels have a slower life history, while meadow-dwelling species under high extrinsic mortality levels have a faster life history. *P. apricenicus*, dwelling in ecosystems with low presence of mammalian predators, shows a long lifespan (skeletochronology) as the rock-dwelling ochotonas. Therefore, we would expect it to move to the slow end of the fast-slow continuum (maturing later and having fewer offspring for its size).

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