Universitat Autònoma de Barcelona

Evolution of body size of extinct endemic small mammals from Mediterranean Islands

BLANCA MONCUNILL SOLÉ

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PhD Thesis
Universitat Autònoma de Barcelona
Doctorate in Biodiversity
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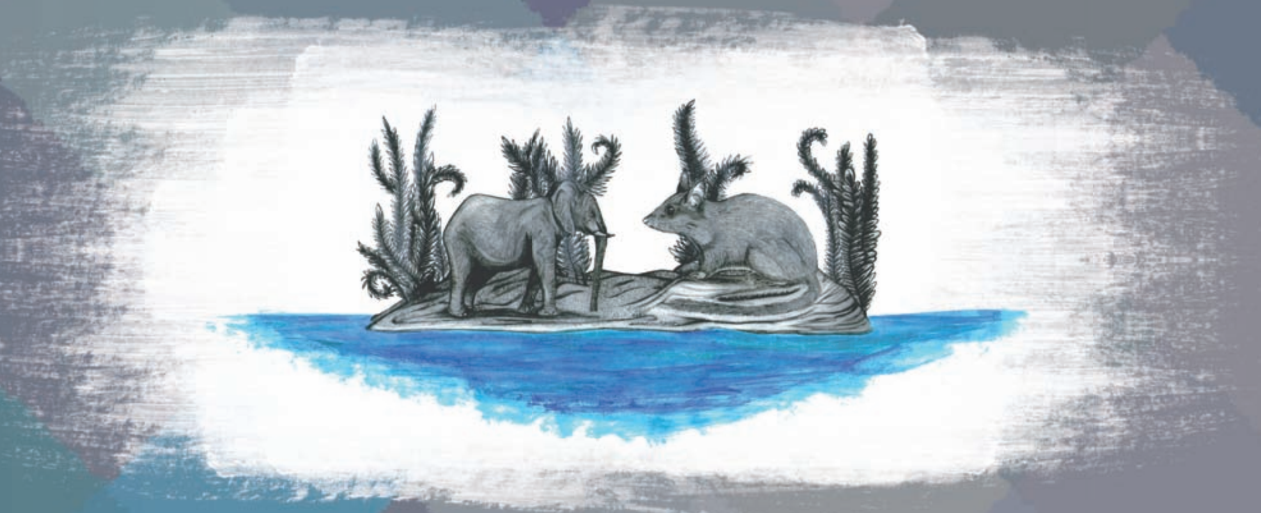
Evolution of body size of extinct endemic small mammals from Mediterranean Islands



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PhD Thesis - 2016

Evolution of body size of extinct endemic small mammals from Mediterranean Islands

Blanca Moncunill Solé

Dissertation presented by Blanca Moncunill Solé in fulfillment of the requirements for the degree of Doctor in the Universitat Autònoma de Barcelona, doctorate program in Biodiversity of the Departament de Biologia Animal, Biologia Vegetal i d'Ecologia. Under the supervision of:

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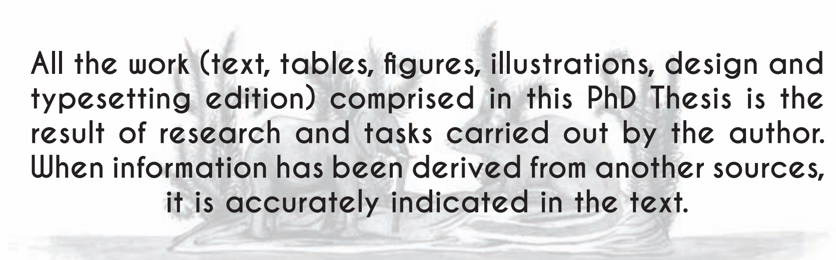

All the work (text, tables, figures, illustrations, design and typesetting edition) comprised in this PhD Thesis is the result of research and tasks carried out by the author. When information has been derived from another sources, it is accurately indicated in the text.

Blanca Moncunill Solé
Bellaterra, June 2016

Where does it come from, this quest, this need to solve life's
mysteries when the simplest of questions can never be answered?
Why are we here? What is the soul? Why do we dream?
Perhaps we'd be better off not looking at all.
Not delving, not yearning.
But that's not human nature. Not the human heart.
That is not why we are here.

Mohinder Suresh (Genesis, Heroes)

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PROLOGUE

Body size (or its proxy: body mass) has a central position in the colossal web of interdependent biological variables of an organism. It shows correlation with lots of physiological, morphological, behavioral, ecological and life history features, and, thus, it affects the fitness of individuals and, ultimately, the biology and evolution of species. The shifts in size (or mass) from an evolutionary point of view are indicative of adaptations to ecosystems through natural selection. So, the vast range of species sizes explains the colonization of almost all Earth niches. One of the most attractive and awesome ecogeographical trends in variation of body size is the well-known Island Rule, where in island ecosystems small mammals (rodents, insectivores or lagomorphs) evolve towards giant morphotypes (relative to their mainland ancestors), while large mammals (elephants, cervids or hippos) towards dwarf morphotypes. Also associated with this size shifts, the insular biotas show characteristic and remarkable morphological, demographic, behavioral, and life history adaptations consequence of the different selective regimens of island (Island Syndrome). The possible causes of Island Rule have always been studied in extant biotas, which lack true endemic native species and have been highly modified by the arrival of humans and invasive species. The extinct biotas are the only ones that can provide a true view and genuine answers for explaining this phenomenon.

The present PhD Thesis attempts to shed light to the Island Rule from a paleontological point of view taking into account the particular evolution of various extinct insular species of the Mediterranean Islands. It is the compilation of the studies carried out at the Evolutionary Paleobiology department of the *Institut Català de Paleontologia Miquel Crusafont* (Sabadell, Spain) during the years 2012-2016. Due to the large amount of mammalian orders, the PhD Thesis is centered in micromammals because the knowledge of gigantism remains widely neglected. The main objective is to make inference on the selection pressures behind the Island Rule taking into account the body mass of the extinct species and the island ecosystem. For knowing the weight of fossil species, several statistical models have been developed using data of current relatives. In this respect and for first time, our results provided allometric regressions for some orders and families of small mammals (Rodentia, Lagomorpha and Soricidae) using various skeletal traits (teeth, skulls and postcranial bones). These new allometric equations not only allow us to make inferences about the Island Rule, but also they can be used in other research fields for knowing better the biology and ecosystems of extinct species. The selective regimes of islands (resource limitation, low extrinsic mortality and interspecific competition) vary from island to island depending on their traits (island area, isolation distance and age) and abiotic factors (climatology or latitude). Each island can be considered as an extraordinary natural laboratory. The traits of each species (phylogeny and phenotypic plasticity) also play an important role in determining the body size shift pattern. In such a way, it has been shown that the pattern (or degree) of gigantism (or dwarfism) is not the same for all insular species.

The present PhD Thesis is structured according to the standards for compendium of publications of the *Departament de Biologia Animal, Biologia Vegetal i Ecologia* of the *Universitat Autònoma de Barcelona* (Bellaterra, Spain), doctorate program in Biodiversity. The "Introduction" chapter (chapter 1) provides the vital and necessary groundwork for following the argumentative thread of the PhD Thesis. It is divided in two main sections: 1) the first describes the paramount role of body size in the biology of species and its broad patterns of variation, and 2) the second supplies the essential framework for understanding the island ecosystems and their selective regimes. Chapter 2 justifies the central issue of the PhD Thesis and covers the proposed objectives for addressing it. The “Materials & Methods” chapter (chapter 3) gives the description of the material of extant and extinct species used and the meticulous statistical procedures carried out for obtaining regression models and for body mass predictions in fossil record. The following chapters (chapters 4 to 9) are the published articles in SCI journals or non-published results in manuscript format. They show the classical structure of a scientific article with a specific introduction, materials and methods, results, discussion and conclusions sections for each one. The “Discussion” chapter (chapter 10) provides a general essay taking into account all the results of the previous investigations. Finally, the “Conclusions” chapter (chapter 11) proposes de main conclusions of the PhD Thesis.

ABBREVIATIONS

BM – Body Mass
BR – Bergmann's Rule
BS – Body Size
CR – Cope's Rule
D_i – Cook's distance
FC – Faunal complex
IC – Interval of confidence
ICP – Institut Català de Paleontologia Miquel Crusafont (Spain)
IR – Island Rule
IS – Island Syndrome
K – Carrying capacity
LH – Life History
LHT – Life History Theory
LH traits – Life History traits
LH strategy – Life History strategy
LOOCV – Leave-one-out cross-validation
MAPE – Mean absolute percent prediction error
MCNM – Museo de Ciencias Naturales de Madrid (Spain)
MSC – Messinian Salinity Crisis
Mya – Million years ago
N – Sample size
NHMUS – Magyar Természettudományi Múzeum (Hungary)
OLS – Ordinary Least Squares, Model I
%PE – Average absolute percent prediction error
r – Intrinsic rate of population growth
r^2 – Coefficient of determination
RE – Ratio Estimator
RMA – Reduced Major Axis, Model II
RMNH – Rijksmuseum van Natuurlijke Historie (Netherlands)
SEE – Standard error of the estimate
SINMNH – Smithsonian Institution National Museum of Natural History (USA)
SSN – Soprintendenza dei Beni Archeologici per le Province di Sassari and Nuoro (Italy)
UB – Universitat de Barcelona (Spain)
UIB – Universitat de les Illes Balears (Spain)
UNIFI – Università degli Studi di Firenze (Italy)
W_M – Weighted mean
$\bar{x}$ – Simple average
$\bar{x}_G$ – Geometric mean

Chapter 1

Introduction

INTRODUCTION

1.1. BODY SIZE

1.1.1. Introduction to body size

Body size (BS) is one of the most fundamental and characteristic biological traits of any organism and is decisive in its evolution (Purvis and Orme 2005, Millien et al. 2006). Through its scaling relationship with other features, BS is considered a key parameter to infer a large diversity of biological aspects (Peters 1983, Calder 1984). It is a trait that is difficult to measure directly in individuals; generally, it is represented by body mass (BM, the weight of an individual in kilograms) at the expense of other proxies such as length, stature or other linear dimensions (Willmer et al. 2005). The current biodiversity of animals covers a BM range from few micrograms (amoeba and rotifer species) to more than one hundred tons (*Balaenoptera musculus* Linnaeus 1758, Order Cetacea), though giant terrestrial species are also known from the fossil record (such as several dinosaurs species and *Paraceratherium* Foster-Cooper 1911, one extinct terrestrial relative of rhinos) (Schmidt-Nielsen 1984, Fortelius and Kappelman 1993, Brown and West 2000, Willmer et al. 2005). Thus, it can be said that BS (or BM) is a fundamental aspect of the extant biodiversity of species.

One of the interesting aspects of BS from a scientific point of view is the variation among individuals. It is shown at different biological levels: among congeneric species, among conspecific populations, and even between sexes of a single population (Harvey and Ralls 1985). Patterns of shift in BS and shape through time can reflect adaptive changes to the environment (abiotic and biotic factors) (Damuth and MacFadden 1990a, Schmidt-Nielsen 1984). Natural selection is responsible of the biological changes of the individuals (including changes of BS, morphology, physiology, among others) in order to optimize the efficiency of species (optimal fitness) depending on the environment (Bonner and Horn 2000). Thus, the extant spectrum of sizes is the co-evolutionary result of adaptations to nearly all of the Earth's ecosystems and environments (Brown et al. 2000). Furthermore, BS plays a crucial role in the biology of individuals. Essential activities and functions, the behavior and ecology of each organism are dependent on it (Brown et al. 2000). It occupies a central position in the immense network of interdependent biological variables, becoming a relevant trait of vital interest. BS covaries with many features of morphology, behavior, physiology, life history (LH) and ecology, such as lifespan, fecundity, interspecific relations or home range (commonly in an allometric way, see below). Given this, the evolutionary changes in BS are expected to be multifactorial and subject to some degree of contingency (Peters 1983, Calder 1984, Schmidt-Nielsen 1984).

In this context, many biological and ecological disciplines recognize the paramount importance of the BS and focus their research on two main fields: 1) understanding the principles, mechanisms and consequences of change in size and scale among similar individuals (see section 1.1.2), and 2) detecting and understanding the patterns of size variation (evolutionary trends) in nature relating them with biological and ecological characteristics of species (see sections 1.1.3 and 1.1.4).

Retrospective review of history in body size's research

Although currently the central and critical position of BS in the biology of species is well-known, research on BS as a main focus did not start until the early 20th century. Thompson (1917), Murray (1926) and Huxley (1932) performed the first studies. They centered on the structural, functional and biological consequences of changes in size and scale, currently coined "scaling" or "allometry" (see below). Geometric relationships and physical principles of mechanics are the basis of their interpretations and explanations. It did not take a long time until BS and its relationship with biological and ecological traits became the subject of interest. The studies of Kleiber (1932, 1961), Brody et al. (1934), Benedict (1938) and Brody (1945) showed that the metabolic rate of mammals (endotherms) scales as the ¾ power of BM (Kleiber's law), in contrast to the geometric scaling idea that metabolic heat production scales as $BM^{2/3}$ (Rubner 1883). Later, it was observed that Kleiber's law also applies to ectothermic or cold-blooded microbes, plants and all animals (Hemmingsen 1960, Gillooly et al. 2001). Studies of the relationship between BM and several biological traits (such as radii of mammalian aortas, mammalian heart and respiratory rates, circulation times for blood mammals, postembryonic development or lifespan) showed exponents multiples of ¼ (investigations summarized in McMahon and Bonner 1983, Calder 1984, Schmidt-Nielsen 1984). It was coined as the "quarter-power scaling" and several theories have been proposed to explain this relationship (McMahon and Bonner 1983, Patterson 1992, West et al. 1997, 1999, Banavar et al. 1999, 2002, Bejan 2000, Darveau et al. 2002, Hochachka et al. 2003). These theories are specific to some biological traits and none of them explains the relationship with sufficient explanatory capacity, power and generality. Particularly, the explanation of the relationships among BS and life history traits (LH traits) lies in the scaling between the adult BS and its metabolic rate. Metabolic rate indicates at which rate the organism is processing energy. Thus, it describes its growth or the total energy allocated to reproduction, and hence the relationship with LH traits. See Maiorana (1990: Fig. 6.6) for the interpretation of the exponents of power functions among LH traits and BM. Contrary to the "quarter power scaling", there are recent studies that observed that basal metabolic rate scales with an exponent less than ¾ (White and Seymour 2003, 2005, McKechnie and Wolf 2004) and suggested that universal metabolic allometry does not exist (White et al. 2006). Regardless of this controversy, Schmidt-Nielsen's research (1984) promoted studies on the scaling of anatomical and physiological characteristics of mammals. Currently, the scaling laws and their related allometric equations are treated as an empirical phenomenon. There are many studies and investigations that treat some measurements of biological structures or processes as a function of BS (or BM) (Millar 1977, Blueweiss et al. 1978, Cabana et al. 1982, Millar and Zammuto 1983, Peters 1983, Calders 1984, among others). One of the most important is the work of Peters (1983), which compiled hundreds of allometric equations that relate BM with biological traits ranging from cellular structure and function to whole organism anatomy (physiology, LH or ecological traits). At present, allometric research is focused on describing empirical scaling relationships (fitting regression equations to data) and developing general theories for explaining these patterns.

Traditionally, changes in BS and scaling in biology have been studied at three different levels: 1) within individual organisms (ontogeny), 2) among different individual organisms and 3) within groups of multiple individuals or species of organisms (populations) (Brown et al. 2000). Firstly, when the variation in size of a simple organism is assessed, it is found that its internal structural units (molecules, macromolecules or cells) remain invariant during changes in BS. These invariant components (structural units) are connected to one another by systems that transport energy, nutrients and other elements, and which provide protection and structural support. Its organization and structure respond to an optimal and efficient design. Therefore, in these cases (such as mammalian circulatory system or branching pattern in plants), natural selection has promoted the evolution of webs with similar, hierarchically scaled architectures (Niklas 1994, Li 1996). Secondly, the studies relating changes in size among individuals belonging to the same or different species is what is known as traditional "allometry" (see below). At present, there is an enormous body of literature concerning the scaling relation between several traits of the individuals (Millar 1977, Blueweiss et al. 1978, Cabana et al. 1982, Millar and Zammuto 1983, Peters 1983, Calders 1984, Enquist et al. 1998, and others). Thirdly, at population and assemblage level, the variation in size is less studied although its high impact on the ecology and evolution (Woodward et al. 2005). Some examples are in the influence of size on the population density, on the diversity of species, on the number of species in a genus or in some other higher taxonomic category, or the species-area relationship (MacArthur and Wilson 1967, Abele 1976, Damuth 1981, Peters 1983, Taylor 1986, Brown and Maurer 1989, Niklas 1994, Brown 1995, Ebenman et al. 1995, Blackburn and Gaston 1997, Enquist et al. 1998, Gaston and Blackburn 2000, Schmid et al. 2000, Kerr and Dickie 2001, Savage et al. 2004, Woodward et al. 2005, White et al. 2007, among others).

1.1.2. Scaling: principles and mechanisms of functionality of live animals

Isometry and allometry

BS is subjected to the universal laws of chemistry and physics, and its variation affects both functional traits of the individual and its relationship with the environment. Thus, it is a critical parameter for the survival of species (Roff 1986, Willmer et al. 2005). When the BS is changed, individuals must adjust their processes and components and compensate the biological and physical consequences in order to continue functioning. This means profound shifts in their structures and functions (Schmidt-Nielsen 1984, Brown and West 2000, Willmer et al. 2005). Three main characteristics can be changed when an organism alters its BS (increases or decreases): the dimensions (e.g. the thickness of the bone or trunk), the material (e.g. material of exo- or endoskeleton) and the design (e.g. the method of locomotion in water or oxygen transportation) (Schmidt-Nielsen 1984, Willmer et al. 2005). The study of these size-related effects among similar organisms is known as "scaling". Some anatomical characters change with size remaining similar (isometric scaling), because the relationship among structures and variables is maintained. But all mammals share the same skeletal architecture and the same organs, but large mammals are not simply magnifications of small ones. In this respect, real organisms are not organized following similar patterns (maintaining the same geometric relationship) due to the powerful constraints (geometrical, physical and biological) imposed on the structures and functions with size change. Most morphological, physiological and ecological traits do not vary as predicted from geometric similarity and they respond disproportionally. They are scaling with BS in a ”non-isometric” or "allometric way" (Schmidt-Nielsen 1984, Brown and West 2000, Willmer et al. 2005) (see chapter 3 for statistical details). However, regardless of organism's size (small or large), they use the same molecules, biochemical reactions, cellular structures and functions in order to survive and reproduce (Brown and West 2000).

The tight relationship among some measurements of biological structures or processes and BS or BM (allometry) can be expressed mathematically by allometric regressions (see chapter 3 for statistical details). These have been widely used in the field of biology with the following goals (Schmidt-Nielsen 1984):

1) To describe a biological relationship.
2) To show how a quantitative variable is related to BS.
3) To disclose principles and connections that otherwise remain hidden.
4) To disclose deviations from a general pattern and make comparisons.
5) To estimate the value of some biological variable for a given BS, including LH and demographic traits.

The last application of allometric regression is of essential use in the paleontological field. Biological traits and processes cannot be observed directly in extinct species, but the relationship to BS makes it possible to reconstruct them.

Body mass: estimations in fossil record

The remains of the fossil record do not directly inform about the BM of an organism. However, estimating the BM of extinct species becomes of vital importance for a profound study of their lives (ecological, physiological, LH, demographic and behavioral parameters) and for understanding their evolution and natural history (Schmidt-Nielsen 1984, Reynolds 2002). The fossil record of vertebrates is represented mainly by bones or teeth, though sometimes soft tissues as skin or biological registers as footprints can also be preserved. These elements allow relatively easy morphological and phylogenetic studies, but inferences concerning biological traits are more difficult to obtain. The design of the skeleton responds to the supporting of weight and loads (preventing the collapse of the organism) and provides levers for movement and locomotion. Consequently, it is directly related to the BM (Schmidt-Nielsen 1984). The narrow functional relationship between skeletal (or teeth) parameters and BM allows us to perform models (isometric or allometric) from extant species. The use of this relationship to the fossil remains allows us to predict the BM of extinct individuals and species (Damuth and MacFadden 1990a). In this respect, several models have been developed to infer the BM of fossil species from different taxa (Legendre and Roth 1988, Damuth and MacFadden 1990a, Gingerich 1990, Anyonge 1993, Christiansen 1999, 2004, Egi 2001, Mendoza et al. 2006, Hopkins 2008, Millien and Bovy 2010, Tsubamoto et al. 2016, among others).

Ruff (2002) emphasized the importance of appreciating the BS (or its proxy BM) and its variation in extinct species. The following points summarize the most significant reasons:

1) The tight relationship between BS (BM) and LH parameters, ecology and social organization allows us to predict these traits in fossil taxa.
2) BS is the usual denominator for assessing key evolutionary trends (such as encephalization, robusticity, among others).
3) BS and the shape of individuals can be used for evaluating geographical and temporal variation.

The BM estimations must be precise and meticulous (Ruff 2002). Under- or overestimating the BM of fossil species could create false images of these organisms or species. For instance, non-accurate BM estimations could cause erroneous inferences of LH traits or deductions of greater or lower mental capabilities of the individuals (taking into account the brain-to-BM ratio, which is understood as an estimation of the intelligence of the organism, though the taxonomic group under study should be taken into account).

1.1.3. Broad patterns in diversification of body size: time and space

One of the most important goals of research in ecology and evolution (macro- and micro-) is to document broad patterns observed in nature and inquire what the responsible mechanisms are (Millien et al. 2006). Thus, the study of the diversification of phylogenetic lineages and the biological changes in traits associated to radiations (such as BS) are steps towards understanding the biodiversity of species (Millien et al. 2006). In the BS field, several trends are recognized in nature taking into account two factors: time and space. We expose the most outstanding below: Cope's Rule (CR), Bergmann's Rule (BR) and Island Rule (IR).

Variation in time: Cope's Rule

CR is defined as the macroevolutionary trend in increasing BS over time (Cope 1887). It is widespread in the animal kingdom from species through genera and families (Benton 1989, Kingsolver and Pfenning 2004). It is explained by the advantages of a larger size: resistance to the short-term variation in physical environment, extraction of energy and nutrients from the poorer-quality food, greater mating success and avoidance of many kinds of predators (Brown and Maurer 1987, Hallam 1975). However, little evidence supports CR at all taxonomic levels or clades, and it has either been dismissed as context-dependent or described as a statistical artefact (MacFadden 1987, Gould 1988).

Variation in space: Bergmann's Rule and Island Rule

These ecogeographical rules basically encompass empirical generalizations, which describe convergences between morphological traits of organisms that evolved under similar physiogeographical conditions (Mayr 1956). The geographical variation of populations or species is not only restricted to changes in BS, but also a complex combination of traits such as variation in color (Gloger's Rule) (Gloger 1833), variation in the length of appendages (Allen's Rule) (Allen 1877) or others (see Millien et al. 2006). In introduced endothermic and ectothermic species, the BS geographic trends may be acquired extremely fast (Schmidt and Jensen 2005, Evans et al. 2012). Generally, the reintroduced species show geographical variation parallel to the ancestral species, which supports the importance of the environment (ecogeography) on species biology (Yom-Tov et al. 1986, Williams and Moore 1989, Huey et al. 2000, Simberloff et al. 2000).

BR is defined as the tendency of individuals of endothermic vertebrates within the geographical range of a species to be larger under colder climatic conditions (Bergmann 1847). Bergmann interpreted it as the selective advantage in higher latitudes and colder climates of the lesser heat loss that accompanies a lower surface-to-volume ratio (Mayr 1956). Although originally it was formulated to describe the latitudinal variation of BS among species of the same genus, at present it is extended within species (Purvis and Orme 2005). The trend is valid for endothermic vertebrates (mammals and birds) (Ashton 2001), but for them, it depends on the phylogenetic group. Some authors observed that chelonians (turtles) follow BR, while squamates (lizards and snakes) and fishes show the converse to BR (BS is negative correlated with latitude and elevation, and hence, it increases with environmental temperatures) (Belk and Houston 2002, Ashton and Feldman 2003, Pincheira-Donoso et al. 2008). In-depth studies showed that other ecological factors (such as moisture, precipitation, primary plant productivity, among others) also correlate with variation of BS in addition to the temperature, suggesting them as responsible for generating the Bergmannian size pattern. Probably, the underlying causes of the variation will be a set of interrelated variables.

IR is initially defined as the general trend for small mammals to evolve towards larger size (giants), while large species evolve towards smaller size (dwarfs) in insular ecosystems (Foster 1964, Van Valen 1973a, Lomolino 1985). However, the IR may be more general than previously suggested: most of the groups of insular non-volant mammals, bats, birds and some reptiles and invertebrates show a trend consistent with this rule with few exceptions (such as carnivores) (Krzanowski 1967, Clegg and Owens 2002, Meiri et al. 2004, Lomolino 2005, McClain et al. 2006, Durst and Roth 2015). Even those species dwelling in insular patches of fragmented forest in mainland ecosystems follow IR (Nupp and Swihart 1996, Schmidt and Jensen 2003, 2005). The IR is also observed in several extinct insular species (Sondaar 1977, Palombo 2007), with extreme cases of gigantism and dwarfism maybe as a consequence of the long period of ecological isolation (Lomolino et al. 2013). However, some authors have pointed out that IR is not a general pattern for all taxa and simply few clade-specific patterns can be identified. They suggested that IR is an artefact of comparing very distant related groups with clade-specific responses to insular regimes (Meiri et al. 2006, 2008, 2011). Dwarfism was initially regarded as a result of a pathological condition due to the interbreeding between individuals of small populations (Leonardi 1954, Kuss 1965). However, the changes of size follow the same pattern on different islands with similar environments, suggesting that it is not random. Thus, the shift in size and other insular adaptations have to be understood as predictable responses to radically divergent selection regimes of the island environment in comparison to the mainland (Sondaar 1977, Lomolino 2005). The BS pattern observed in island environment may not result from one single factor, but from a combination of convergent forces (McClain et al. 2013).

In the section 1.2 (Islands) of this chapter, a more exhaustive framework of the IR is given including a first section of contextualization and subsequent sections about the general biological changes of insular dwellers and the principles that some authors proposed as drivers of the IR.

1.1.4. Biology and ecology of body size

Community ecologists have always suggested that BS is the primary target of natural selection, and, thus, the patterns of biological characteristics of an individual are the consequence of variation in its adult BS (Wester 1979, 1983, Western and Ssemakula 1982, among others). However, recently, a new perspective has been established in this field. Variation in BS may also be interpreted as a consequence of changes in the LH (and its traits) of individuals. Thus, the observed BS changes are not a direct result of selection, but instead selective pressures may alter the elements of an organism's LH to which the BS of an adult is sensitive (Stearns 1992, Palkovacs 2003). The following subsections go deeper into these two fields in detail.

Selection pressures operating on body size: benefits and costs of large and small sizes

Different selection pressures are the evolutionary forces that determine the BS of organisms (Blanckenhorn 2000, Bonnet et al. 2000). Fecundity and sexual selection tend to trigger size increase because large organisms have greater reproductive and mating success and produce offspring of better quality (Clutton-Brock 1988, Andersson 1994). Meanwhile, natural selection is also involved in the evolution of BS in order to maximize organismal survival and change their growth trajectories. The viability or survival selection acts improving the probability of survival until adulthood, a life stage very susceptible where the organism is already breeding and can have offspring. In such a way, it encourages small sizes (Andersson 1994). Evolution of BM (phenotypic trait) is the result of the balance between the fitness advantages of these opposing and conflicting pressures, which depend on the different selective regimes (Schulter et al. 1991). For more details of mechanisms of selection for and against BS see Blanckenhorn (2000).

Thus, BS has consequences for an animal's biology and its relationship with the ecosystem in the form of fitness benefits (advantages) or costs (disadvantages) (Hone and Benton 2005). The benefits of large-sized species will be the costs that small-sized organisms have to assume (e.g. larger size allows a greater range of acceptable foods; small-sized organisms have the disadvantage of having a more reduced range of acceptable foods), while the assumed costs of a larger size will be the benefits of a small-sized organism (e.g. large size organisms have greater food requirements; the lower food requirement of small-sized organisms is a benefit). In general, large-sized animals are better predators and increase their defense against other predators. Also, their range of acceptable foods is greater and their survival is higher during food paucity periods (Sinclair et al. 2003). The mating, reproduction, intra- and interspecific competition success is higher in large-sized animals (Clutton-Brock 1988). Biologically, they show an extended longevity and an increased intelligence (consequence of the brain size increment associated to the increase of BM) (Roff 1992). Particularly in the case of large-sized endotherms, they devote less energy and metabolism relative to BM to maintain body temperature, displaying a better thermal efficiency. Small endotherms have a large surface to volume ratio, losing much more energy as heat compared with the large ones (McNab 1983, 2002a, 2012, Willmer et al. 2005). On the other hand, larger sizes also have biological disadvantages. Large-sized animals increase their development time at both pre- and postnatal level. Their food, water and energy requirements are higher (Clauss et al. 2013). As a result, the population densities are reduced and show susceptibility to extinction (Beissinger 2000). Their longer generation times give a slower rate of evolution and a reduced ability for adapting to rapid and unexpected changes of the environment (Brown 1995).

Allometric relationship among life history and body size

LH is known as the amount of succeeding stages and key events, which an organism passes throughout its lifetime. It is defined by the LH traits, a set of biological characters (which include longevity, fecundity, age at maturity, offspring size, among others) considered as fitness components (Stearns 1992). The combination of LH traits of an organism affects the individual's survival and reproductive potential and defines the individual fitness, the population growth and the species' competitive ability (Schulter et al. 1991, Stearns 1992, Roff 2002). BS (or BM) shows an interesting allometric correlation with LH and LH traits (Blueweiss et al. 1978).

The ensemble of LH traits of a given individual (population or species) for maximizing fitness in a specific environment is termed as life history strategy (LH strategy) or pattern (Cole 1954). Initially, MacArthur and Wilson (1967) proposed two main LH selections (ultimately, species) depending on the environment (selection pressures): *K*-selection (equilibrium species) and *r*-selection (opportunistic species). In populations that dwell in environments that are unstable or subject to extreme variations, mortality of individuals is independent of density and of individual competitive abilities. In these scenarios, the selection would stimulate the exponential growth of the population and favor traits and features that maximize *r* (intrinsic rate of population growth). Thus, we talk about *r* LH strategy or species. In contrast, in stable and constant environments, population density saturates at carrying capacity (*K*). At high population densities, *r* decreases and individual mortality becomes density-dependent. In other words, mortality would differentially affect individuals depending principally on their efficiency in the acquisition of resources. Thus, selection encourages a maximized efficiency in resource acquirement and greater competition among individuals. In such cases, we talk about *K* LH strategy or species. Later, Pianka (1970) described the *r-K* continuum and characterized biologically the extreme endpoints. Generally, *r* environments are resource-rich, non-competitive, uncertain and unpredictable. In this type of environments, the mortality is catastrophic (density-independent) and the population size is not in equilibrium. Selection favors species (*r*-species) of rapid development, early reproduction (high reproductive effort), semelparity (single reproduction) and a short lifespan. They are species of small BS. In this case, these environments encourage high productivity selecting traits that enhance population growth. On the other hand, *K* environments are typically more predictable, resource-limited and competitive. In this case, selection favors species (*K*-species) of slower development (investment in maintenance), delayed maturity and low fecundity (low reproductive effort), iteroparity (repeated reproductions) and a long lifespan. Their population size is constant in time and the mortality is density-dependent. Characteristically, they are species of large BS. These predictable environments lead to efficiency of utilization of environmental resources (Pianka 1974, Reznick et al. 2002). The tight allometric relationship between LH variables and BS let some researchers suggest that the LH differences among species are a consequence of selection for different sizes (Lindstedt and Calder 1981, Western and Ssemakula 1982). However, later observations showed that LH traits co-vary in a systematic way when the effects of BS are removed (Stearns 1983).

The *r-K* selection is simple (it does not take into account which age ranges or classes are affected by the mortality) and does not have much empirical evidences. As a result, the study of LH evolution and Life History Theory (LHT) was initiated (Gadgil and Bossert 1970, Charnov and Krebs 1973, Schaffer 1972, Stearns 1976, 1977, 1983, 1989, 1992, Roff 1992, among others). LHT suggests the vital role of the age-specific extrinsic mortality as the mechanistic link between an environment and the optimal LH (for a more exhaustive revision see Reznick et al. 2002), in contrast to *r/K* theory of MacArthur and Wilson (1967). The study of the evolution of LHs and LHT attempts to understand the variation and adaptation in LH strategies based on quantitative genetics, population ecology and physiology (Roff 1992, 2002, Stearns 1992). The comparative LH investigations developed during this last half century have suggested the idea of a fast-slow continuum where any mammalian population can be placed along it (Read and Harvey 1989, and references therein). Species at the fast end of the continuum have an early maturation, a large reproductive rate, short longevity and generation times. At the other end of the continuum, the slow one, the species have an opposite suite of traits (Read and Harvey 1989, Promislow and Harvey 1990).

LHT is supported by the concept of energy allocation and trade-offs (Dobzhansky 1950, Fisher 1958). Energy captured by organisms is limited in absolute and relative terms (Kozlowski and Wiegert 1987). According to LHT (Roff 1992, Stearns 1992), individuals must assign their resources and energy across different vital tasks, so that the energy devoted to one activity cannot simultaneously be devoted to another one (Cody 1966, Roff 2002). To that extent, energetic trade-offs (constraining relationships) are established among several vital functions: reproduction, growth, maintenance, storage, among others. One of the most fundamental trade-offs is between reproduction (immediate) and growth (somatic efforts for survival and future reproduction) (Williams 1966). This trade-off determines large or small BS: large-sized organisms (*K*-species) allocate the resource energy to maintenance and growth, increasing survival and future fitness at the expense of current fitness. They increase their development time to maturity having longer generation times. On the other hand, small mammals (*r*-species) allocate the resource energy to reproduction increasing immediate fitness (Stearns 1992). LHT pointed out that selective pressures may act directly on LH traits (fitness components) in order to maximize life time reproduction. The alteration of traits and elements of an individual's LH may trigger changes in BS, due to the BS sensitivity. This general explanation suggests that LHT may be a better predictor to account for some BS patterns, such as IR (Palkovacs 2003). For more details see section 1.2.3.

1.2. ISLANDS

1.2.1. Introduction to islands: Mediterranean Islands

Islands are considered evolutionary and ecological units. Each of them is an extraordinary, unique, and natural laboratory, differing in total surface, degree of isolation (proximity to the mainland), geological age, and diversity and intensity of the ecological interactions (number of species, competitors, among other traits) (Whittaker 1998, McNab 2002b). Islands offer a series of repeatable and testable experiments for assessing and understanding biogeographical, ecological and evolutionary processes (MacArthur and Wilson 1967). Islands are not only considered lands surrounded by water (sea islands), but also discrete patches of terrestrial habitat surrounded by different habitat that is not necessarily water (habitat islands) (Whittaker 1998, Schmidt and Jensen 2003, 2005). Two different types of islands are identified according to their origin: 1) continental and 2) oceanic (Darlington 1957). On the one hand, continental islands are part of the mainland shelf and their isolation is consequence of subsidence of the isthmus of a peninsula or sea level fluctuations. On the other hand, oceanic islands (true islands) arise from beneath the sea and they have been surrounded by deep water since their origin. They are of volcanic or coralline formation, and all organisms (plants and animals) immigrated oversea from elsewhere. Alcover et al. (1998) described the new category oceanic-like islands, in reference to those continental islands that were connected to the mainland in the past and have remained isolated for a long time. In general, oceanic islands are those for which evolution is faster than immigration, while continental ones are those where immigration is faster than evolution. Sometimes this simple categorization is difficult to apply to reality (Darlington 1957, Carlquist 1974). The geological scale allows us to infer the history of islands and modifications in their category (such as temporal periods where the island is joined to the continent, submerged or isolated) (Marra 2005, 2013). Faunal complexes (FC, a set of local faunal assemblages spread in a certain time span and having coherent taxonomic and ecologic features) in each geological moment are a reflection of these changes and are used as a paleogeographical tool (Whittaker 1998, De Vos et al. 2007, Van der Geer et al. 2010). The dispersal of biota to the island can be carried out via three media: 1) over land, 2) over water or 3) through the air. The first type is restricted to land organisms and comprises the corridor (land bridge) and filter dispersal (including short distance over water). The second type is limited to organisms that can swim, float or raft on a floating mass. The sweepstake dispersal, over natural rafts or masses of vegetation, is considered feasible for terrestrial small mammals to cross masses of water (Honacki et al. 1982). Large mammals with swimming abilities (such as elephants, deer and rhinos) can reach nearby islands (Sondaar 1977). The third type is limited to flyers. This explains the presence and colonization of terrestrial mammals of some isolated oceanic islands. “Over land” is the typical dispersal route that organisms used to reach continental islands, while “over sea” or “through air” have a key importance for populating oceanic islands (Alcover 1987, Van der Geer et al. 2010). Other routes of colonizations are described in Alcover (1987). The FC that found on an island reflects the balance between the migration of new species towards the island and the extinction of endemics (MacArthur and Wilson 1967).

Some of the most characteristic and interesting islands are those situated in the Mediterranean Sea, which is located between Southern Europe, Anatolia, Levant and North Africa and is connected to the Atlantic Ocean solely by the Strait of Gibraltar (Goffredo and Dubinsky 2014). Around the latitude 40ºN, the climate of areas bordering the Mediterranean Sea is very characteristic and homogeneous. Currently, it is described as biseasonal: mild, rainy winters and hot, dry summers (Lulla 1998, Peel et al. 2007). Among the several islands that are found there, it is worth mentioning (approximately from largest to smallest): Sicily (Italy), Sardinia and Corsica (Tyrrhenian Islands, Italy and France respectively), Cyprus, Mallorca and Menorca (Gymnesic Islands, Spain), Aegean Islands (Euboea, Lesbos, Rhodes, Chios, among others) where Crete stands out for its larger area (Greece), Ibiza and Formentera (Pityusic Islands, Spain), and Malta, among others (Vogiatzakis et al. 2008). Fluctuations of the sea level and tectonic movements caused the disappearance or integration in a larger landmass of some islands that existed in geological times, such as Gargano and Baccinello (Italy) (Freudenthal 1971, Hurzeler and Engesser 1976, Masini et al. 2010). One of the most dramatic geological events that occurred in the Mediterranean Sea, and which influenced the biota composition of these islands, is the Messinian Salinity Crisis (MSC) (in the Late Miocene, 5.6 Mya). It consisted of a desiccation of the Mediterranean Sea as a result of the closure of the Strait of Gibraltar (connection across Spain and Morocco) and posterior evaporation at a very fast pace (Hsü et al. 1973, Krijgsman et al. 1999). This event had two consequences: 1) the lands previously submerged by the Mediterranean Sea became new sites of colonization, and 2) a land bridges were created allowing faunal exchange between different mainland parts or with previous island zones (Alcover et al. 1981). Later (5.33 Mya), the Mediterranean Sea was refilled (Zanclean Flood) with water from the Atlantic Ocean when the Gibraltar Strait was opened (Blanc 2002). In this way, the islands were isolated again with a new faunal contribution from the mainland. Some of these islands, such as Mallorca and Menorca, did not have posterior colonizations of terrestrial fauna and remained in isolation for around 5 million years until the arrival of humans (Bover and Alcover 2008, Bover et al. 2016); while others had faunal interchanges with the mainland (land bridges, sweepstake, or filter dispersal) having different FCs, such as Sardinia or Sicily (Marra 2005, 2013). For more details of FCs of Mediterranean Islands see chapter 3.

1.2.2. Insular faunas: Island Rule and Island Syndrome

Generally, the biotas (flora and fauna) hosted on islands are impoverished (low number of species), unbalanced or disharmonic (absence of important families or higher taxa) and endemic with regard to the mainland ones. It is commonly suggested that the area (resources and energy availability) and isolation distance (immigration potential) play a key role in determining their biodiversity and species richness (Sondaar 1977). Generally, permanent isolation allows allopatric speciation and presence of endemisms (biological taxon with characteristic traits and within a unique and well-defined geographical area) and some islands become true biodiversity hotspots (biogeographic region with significant reservoirs of biodiversity) (Whittaker 1998). What is most interesting about the biotas from islands is that their organisms show unique and special biological, morphological and behavioral traits. Typical examples are herbaceous plants in form of trees, birds and insects that have lost the power of flight, and, as mentioned previously, the presence of dwarfs and giants of several vertebrate groups (IR, see section 1.1.3) (Darlington 1943, Foster 1964, Ricklefs and Cox 1972, Olson 1973, Carlquist 1974, Mabberley 1979, Alcover et al. 1981, Grant and Grant 1989, Roff 1990, 1994, Knox et al. 1993, Knox and Palmer 1995, 1996, Böhle et al. 1996, Cody and Overton 1996, Bowen and Van Vuren 1997, Grant 1998, Roots 2006, Mayol 2009, Medeiros and Gillespie 2010, Van der Geer et al. 2010, Kavanagh and Burns 2014, Mageski et al. 2015, among others).

MacArthur and Wilson (1967) were the first in studying the species' richness on islands (insular biogeography). They put forward the *r/K* theory of density-dependent selection for the regulation of insular populations (see section 1.1.4). According to them, the degree of isolation and the interrupted gene flow are the most important factors. They suggested that during colonization the population is only slightly affected by density, and it is growing. In this initial stage, selection stimulates those genotypes of individuals that have the effect of maximizing the *r* (productivity) (see section 1.1.4 for the features of this kind of strategy). Later, in a few generations, the population achieves carrying capacity (*K*) (due to the particular selective regimes of islands). In this moment, selection favors genotypes that are relatively unaffected by high population densities. In other words, it favors *K* strategists (efficiency) (see section 1.1.4 for this kind of strategy). In agreement with *r/K* theory, subsequent studies have shown that insular populations of mammals are distinguished by differences in their demography, LH (reproduction and survival), behavior and morphology (Adler and Levins 1994, Lloyd 2011). The same pattern, regardless of the taxon, arises in several insular populations of different species and from diverse geographic areas. Thus, this set of traits, extending far beyond BS variation, is termed the Island Syndrome (IS) and it is a direct consequence of the insularity (Adler and Levins 1994, Blondel 2000). From a demographic point of view, insular populations of small mammals have higher and more stable densities, which increase with the degree of island isolation and decline when the island size is increased (as suggested by MacArthur and Wilson 1967). They present a shift towards a slow life history (*K* strategy): higher survival rates and reduced reproductive outputs. Moreover, they are also characterized by systematic differences in behavior (Adler and Levins 1994).

Morphologically, the convergences observed among mammals of different insular FC is impressive (for a review see Van der Geer 2014, Jordana et al. 2015). In general, regardless of their BS, they are characterized by low gear locomotion, increased hypsodonty, small size of areas of the skull related to the senses and traits that improve the capacity to acquire fallback foods (resources of poor nutritional quality that become essential when preferred aliments are scarce) (Sondaar 1977, Köhler and Moyà-Solà 2004, 2011, Van der Geer 2014). Dwarf insular mammals (ruminants, hippos and elephants) show a shortening and thickening of the distal part of the leg (distal limb bones and phalanges) and, in some cases, fusion of some of the foot bones (Leinders and Sondaar 1974, De Vos 1979, Moyà-Solà 1979, Klein Hofmeijer 1997, Van der Geer 2005, for a review see Van der Geer 2014). It becomes a solid construction that is advantageous for low speed locomotion in rocky environments and disadvantageous for escaping predators (loss of speed and zigzag movement) (Leinders 1976, Leinders and Sondaar 1974, Moyà-Solà 1979). These modifications allow the center of gravity to lower, implying more stability for the animal (Sondaar 1977, Alcover et al. 1981, Köhler and Moyà-Solà 2001, Scarborough et al. 2015). Especially in the proboscideans (elephants), a lack of strong pneumatization of the skull is observed (Accordi and Palombo 1971, Palombo 2001). In small running and jumping mammals, such as rabbits, several adaptations are also observed, such as a stiff vertebral column, low sacropelvic angles, among other traits, for low gear locomotion (Yamada and Cervantes 2005, Quintana et al. 2011). Typically, large and small insular mammals show loss or reduction of dental pieces (incisors, premolars and molars) and an increase in hypsodonty (Alcover et al. 1981, Jordana et al. 2012, Van der Geer 2014), which may be related to a more abrasive diet (Sondaar 1977, Schüle 1993, Angelone 2005) but also to an extended longevity (Köhler 2010, Jordana et al. 2012) and a high intraspecific competition (Casanovas-Vilar et al. 2011). Moreover, insular pikas and murids show more complex enamel patterns (Angelone 2005). Some insular species display small orbits in frontal position or brain size reduction (Köhler and Moyà-Solà 2004, Bover and Tolosa 2005, Palombo et al. 2008, Weston and Lister 2009, Quintana et al. 2011; in contrast see the tendency of elephants in Palombo 2001, Larramendi and Palombo 2015). Moreover, they exhibit morphological traits for searching for fallback foods under low resource conditions, adaptations for digging and scrabbling the ground and a more specialized dentition for a generalized and abrasive diet (Parra et al. 1999, Köhler and Moyà-Solà 2004, Hautier et al. 2009, Quintana et al. 2011, Michaux et al. 2012, Quintana Cardona and Moncunill-Solé 2014). Additionally, some extinct insular species are distinguished by a large variation in BS (Roth 1993, Taruno and Kawamura 2007). In the cases where islands entail a breadth of niches for species, insular natives may undergo typical evolutionary transformations for occupying new ecological positions (Palombo 2007, 2009a, Losos and Ricklefs 2009). In such a way, birds of oceanic islands decrease their energy investment for flight muscles and converge in the ecological strategy and bauplan of large, herbivorous non-volant vertebrates such as ungulates when they are not present on the island (McNab 2002b, 2009, 2012, 2013).

These repeated evolutionary patterns in mammals of different islands can be explained as adaptations to the island environment due to their different selective regimes (general absence of terrestrial predators and resource limitation) (Foster 1964, Sondaar 1977) (see section 1.2.3). The adaptive process can be split in two overriding stages differentiated in their realization time. The first stage is in the evolutionary direction (principally, energy saving by low gear locomotion, BS shift, and others changes) and occurred in a relatively short time. Recently, Evans and collaborators (2012) estimated around (at least) 4000 years for a small mammal to undergo gigantism (16000 generations), and around 25000 years in large mammals, such as elephants, to undergo dwarfism (1000 generations). The next stage is allowing the continuation of the direction of the first change (principally increase of hypsodonty, changes in dentognathic feeding apparatus or developing traits for searching for fallback resources) (Sondaar 1977, Alcover et al. 1981, Lister 1989, 1996, Köhler and Moyà-Solà 2004, Lomolino et al. 2013). Accordingly, Mein (1983) described the evolution of islands by two periods with different evolution rate. Firstly a tachytelic stage takes place (evolution at rate faster than the standard ones), and later a long bradytelic stage (evolution at rate slower than the standard ones). This model has been corroborated by several studies (Millien 2006, Cucchi et al. 2014, Aubret 2015, García-Porta et al. 2016; for contrast opinion see Raia and Meiri 2011), which have observed that following colonization the morphological changes on islands occur rapidly (accelerated rate of evolution) and later on the populations show a stasis corresponding to a demographic equilibrium and a local optimum. In this respect, studies on extant rodents reported extremely high rates of microevolution (100 years), particularly on smaller and more remote islands (Pergams and Ashley 2001).

The evaluation of IR and IS in large mammals is difficult as a consequence of the current absence of endemisms on islands, in contrast to small mammals (Austad 1993, Adler and Levins 1994, Adler 1996, Anderson and Handley 2002, Lambert et al. 2003, Salvador and Fernandez 2008a, Barun et al. 2015, Gray et al. 2015, among others). However the Miocene and Plio-Quaternary faunas of the Mediterranean Islands are good examples of the modifications mentioned above. Dwarf insular mammals include elephants [e.g. *Palaeoloxodon falconeri* (Busk 1867), *Palaeoloxodon mnaidriensis* (Adams 1874), *Palaeoloxodon cypriotes* (Bate 1904)], hippopotamus [e.g. *Phanourius minor* (Desmarest 1822)], bovids (e.g. *Myotragus* Bate 1909, *Maremmia* Hurzeler and Engesser 1976, *Nesogoral* Gliozzi and Malatesta 1980), cervids (e.g. species of *Candiacervus* Kuss 1975, *Cervus elaphus siciliae* Gliozzi et al. 1993), among other taxa. On the other hand, giant species comprise lagomorphs (e.g. *Nuralagus rex* Quintana et al. 2011, *Prolagus imperialis* Mazza 1987, *Prolagus sardus* Wagner 1832), rodents [e.g. *Hypnomys* Bate 1919, *Kritimys* Kuss and Missone 1968, *Mikrotia* (Freudenthal 1976)] and insectivores (e.g. *Deinogalerix* Freudenthal 1972, *Nesiotites* Bate 1945), among other taxa (Van der Geer et al. 2010). One of the most investigated and well-known extinct dwarf mammals is the caprine *Myotragus balearicus* Bate 1909 and its anagenetic lineage from Gymnesic Islands (Mallorca and Menorca, Spain) (Alcover et al. 1981). Its exceptional fossil record places it in the central point of investigations in the field of islands. It is suggested that this species reached maturity at about 12 years, showed an extended longevity (35 years) and gave birth to neonates of low weight with a high degree of immaturity. According to the *r/K* theory, these facts indicated that this species shifted towards a very slow LH (Köhler and Moyà-Solà 2009, Köhler 2010, Marín-Moratalla et al. 2011, Jordana et al. 2012). On the other hand, several morphological modifications in the genus are indicative of a stable, low gear and energetic-saving locomotion (Moyà-Solà 1979). It is characterized by a reduction of the brain mass, orbits, olfactory bulbs, olfactory nerves and foramen magnum (Köhler and Moyà-Solà 2004). Particularly, *M. balearicus* shows a reduced capacity of raising the neck beyond the shoulders, a reduced thorax (reduced pulmonary capabilities) and wings of ilium in horizontal position (voluminous digestive system) (Köhler and Moyà-Solà 2004). Gradually, the anagenetic lineage of *Myotragus* species incorporates several specific dental traits: a reduction of the number of teeth, increase of the molar hypsodonty and the presence of ever-growing and open-rooted lower incisors of permanent dentition (hypselodont incisors) (Alcover et al. 1981). Moreover, *M. balearicus* shows a slow signature of dental eruption sequence in comparison with extant bovids, that suggests a slow LH (Schultz's Rule) (Jordana et al. 2013). For more details of FCs of Mediterranean Islands see chapter 3.

However, this peculiar and impressive fauna, adapted to their particular ecological regimes, is very vulnerable to the entrance of new immigrants. Thus, when new colonizers (predators or competitors) are introduced in the islands, they cause, generally, the extinction of the native taxa leading to substitutions of the biota (Donlan and Wilcox 2008). In the past, direct connections or the proximity to the coastline allowed the arrival of faunal waves to the islands and natural extinctions (Marra 2005). However, nowadays, of particular importance was the entrance of humans (transforming the habitat or introducing diseases, predators and competitors) and invasive species (producing exclusion of local species by competition, displacement of niches, hybridization, introgression, predation and ultimately extinction) to natural virgin ecosystems of islands (Mooney and Cleland 2001, Bover and Alcover 2008, Masseti 2009, Bover et al. 2016). McNab (2002b) defined very precisely the human's influence on islands: «*Humans have all but eliminated the "fantasy" world on oceanic island... We are converting islands into minicontinents, thereby facilitating the irrevocable loss of species that would contribute to our understanding of the responses of life to environments liberated from the tyranny of mammalian predation*». In this respect, Sondaar (1987, 1991) pointed out that the peculiar and striking traits of insular species that we find in the fossil record could not have evolved and coexisted with humans, due to their susceptibility to human influence (directly, such as hunting, or indirectly, such as habitat alteration or introduced species). While the size of the human population continues to grow, the spatial patterning, structure and function of most ecosystems of the world, including islands, will continue to be altered by the human activities affecting the atmosphere and the climate. A new cosmopolitan assemblage of organisms is settling down on the entire surface of the Earth, which will have enormous consequences not only for the functioning ecosystems but also for the future evolutionary trajectory of life (Mooney and Cleland 2001).

1.2.3. Insular ecosystems: a new ecological regime

In any ecosystem, the energy from the sun is the essential element that allows the functions, movements, and vital cycle of organisms and, in absolute terms, life, as we know it. Plants, algae and some bacteria, termed as photosynthetic organisms, are capable of transforming the sun light to energetic organic matter, being of paramount importance in the ecosystems. Animals and other non-photosynthetic organisms have to consume primary producers or other animals for obtaining energy. In this way, a food chain for gaining energy is established. The complex process of capturing light limits the total energy obtained, and, moreover, energy is partially lost along the food chain as a consequence of metabolic activities of organisms. This is generally depicted in form of an energy pyramid. In the case of islands, their small surface results in a low number of primary producers and less energy, conditioning and limiting life. The limited and reduced energy in islands prevents a high rich fauna and the presence of several taxa, especially those of the top of the energy pyramid such as carnivores, and natural selection favors those economical individuals (organisms that need fewer resources for surviving), such as ectotherms (McNab 1994a, 1994b, 2001, 2002a, 2002b, 2009, 2012, Köhler and Moyà-Solà 2011). Thus, from an ecological point of view, the simple ecosystems of islands are characterized by a limited primary productivity (a consequence of the geographic limitations of islands), an overall lower predation pressure (consequence of the general absence of mammalian predators) and high intraspecific competition (Sondaar 1977, Heaney 1978) (Fig. 1.1).

The reduced available energy of islands is paramount to explain the adaptation of their populations. To explain the IR, several hypotheses are proposed highlighting three specific ecological factors of islands: competition, predation and resource availability (Lomolino 1985, 2005, Grant 1998, McNab 2002b), which may act as direct selection pressures on the BS of the individuals (see section 1.1.4). The interspecific competition on islands is reduced as a consequence of the low richness of species of islands (MacArthur and Wilson 1967). In these conditions, several authors (Van Valen 1965, Lister 1976, Heaney 1978) indicated that the breadth of niches is greater and the small-sized species, which now live on islands, can eat large and small food items. This may foster an overall increase in size of the small species (gigantism). On the other hand, it is also true that predation on islands is less than on the mainland and the populations are released from this selection pressure (Foster 1964, Sondaar 1977, Heaney 1978, Adler and Levins 1994). With regard to this, several authors (Sondaar 1977, Heaney 1978, Lomolino 2005) proposed that this pressure release may encourage small mammals, which escape hiding from predators, to increase its size (gigantism); and large mammals, which confront running or fighting predators, to decrease its size (dwarfism). Finally, the resource limitation of islands affects basically large bodied mammals. They require more energy intake, and accordingly

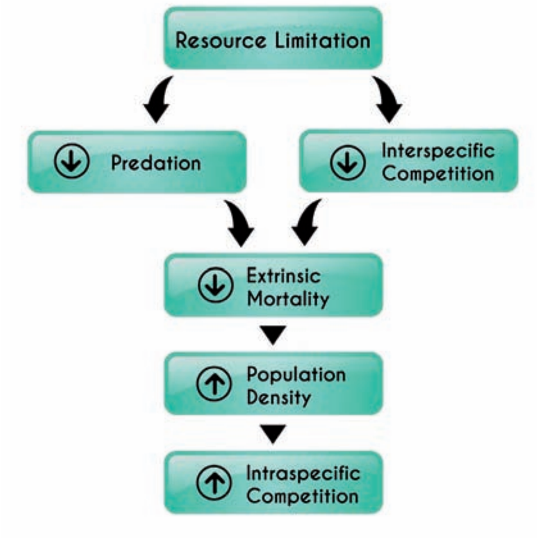

Figure 1.1. Diagram of the ecological characteristics of islands, modified from Köhler and Moyà-Solà (2011). Islands are defined by a reduced area and, thus, by resource limitation. As a result of this, carnivorous predators are absent and there is lower species richness (lower interspecific competition). These two traits produce a lower extrinsic mortality than mainland. The population density increases and, consequently, the intraspecific competition too.

it is suggested that they adapted to it with a small size morphotype (dwarf) (Foster 1964). In this respect, Lawlor (1982) suggested that, in small mammals, the effect of resource levels of islands is different for specialist or generalist species. It is taken into account that the former group exploits patchy resources on the island and, consequently, has greater competition. In this way, a large BS for generalist species and a small BS for specialists should be favored (Lawlor 1982). This is supported by Durst and Roth (2015), who have observed that resource limitation is the major driver in the few cases of dwarf insular rodents (e.g. species of *Perognathus* Wied-Neuwied 1839 on the islands of Central America). Thus, the selection pressures on insular BS are phylogenetically and ecologically context-dependent (McClain et al. 2013). In other words, the responses to selective regimes of islands depend on the particular species and the spatial and temporal scales (Lomolino 2005: Fig. 9). Consequently, of these particular regimes, the species-poor communities show few or sole resident species converging on intermediate BS in contrast to species-rich mainland systems (with ecological displacement and diversification of species) (Lomolino et al. 2012).

These three primary factors (predation, competition and resource) depend on characteristics of the island such as degree of isolation, area and other factors that influence resource levels, productivity, species diversity (number), climatic factors, ecological interactions and the likelihood of colonization, affecting the BS and other features of insular populations (Adler and Levins 1994, Lomolino 2005, Palombo 2009a, Lomolino et al. 2012, 2013, Durst and Roth 2012, 2015). BS of mainland ancestor, diet or lifestyle abilities also conditioned the BS shift and its direction in large and small mammals (Lawlor 1982, Lomolino et al. 2012, 2013, McClain et al. 2013, Durst and Roth 2012, 2015). In this respect, Meiri et al. (2008) suggested that the BS evolution on islands depends largely on biotic and abiotic traits of islands, the biology of the species and contingency, but that the IR is not a rule *per se* (see section 1.1.3). In the case of small species, several authors have observed that gigantism is more pronounced for populations dwelling on smaller and moderately isolated islands without the presence of mammalian competitors and predators (Lomolino et al. 2012, Durst and Roth 2015). On the other hand, scientific studies (Palombo 2009a, Lomolino et al. 2012) suggested that the degree of isolation and area of island does not seem to influence the degree of dwarfism *per se* in large mammals, which is conditioned by the presence of competitors and predators and the types and diversity of resources. The studies of Lomolino et al. (2012) evinced that the latitude and climate are also factors that must be considered to explain the degree of gigantism, but not of dwarfism. In fossil species it is observed that the small mammals evolve towards larger size when neither mammalian competitors nor predators are present, while with the presence of new settlers (mammalian competitors or predators) the trend is less pronounced or reversed (Van der Geer et al. 2013). Also the climatic oscillations at geological scale may fluctuate the BS of insular species. For instance, warming environmental conditions promote smaller BS, which is in contrast to the IR trend for small mammals (Van der Geer et al. 2013). Some authors (McClain et al. 2013) suggested that the direction of BS shift on islands is linked to the evolutionary history of the species (BS of ancestor, trophic level and climatic niche) but the degree of change is influenced by mainland range and species' climatic niche breadth. However, many exceptions are known and not all populations dwelling on islands show the pattern expected by the IR and the IS. Insufficient island isolation (presence of a flow between island and mainland exists), too large or too small island size (with selective regimes more similar to those of mainland), or other factors can explain its absence (Heaney 1978, Adler and Levins 1994).

Alternative explanations for IR are based on the adaptive changes in age and size at maturity of insular dwellers and depend primarily on the relative importance of the lowered extrinsic mortality rate and limited resource availability (Palkovacs 2003) (Fig. 1.2). According to *r/K* theory and LHT, this new regime alters traits of the LH of individuals (LH strategy) and, indirectly, the BS in order to maximize their fitness (Palkovacs 2003). Increase or decrease in BS rely on the predominance of resource limitation (adult BS decrease) or reduced mortality (adult BS increase) (Palkovacs 2003). In large mammals, the resource limitation is of greater importance than the reduced extrinsic mortality. This supposes a large drop in the growth rate resulting in a net decrease of BS (Fig. 1.2). On the other hand, small mammals are more heavily influenced by lower extrinsic mortality, and lesser by the resource limitation of the islands (maintaining their growth rate). According to the LHT, the lower mortality rate entails an increase in the age and BS at maturity. Consequently, these species increase fecundity (number or size) (Fig. 1.2). Several empirical evidences exist supporting this theory (Palkovacs 2003). In this theoretical framework, paleontological research suggests energy allocation to growth and maintenance and a shift towards a slow LH strategy for large and small insular mammals (Köhler and Moyà-Solà 2009, Köhler 2010, Jordana and Köhler 2011, Orlandi-Oliveras et al. 2016). On the other hand, taking into account the scaling concepts, other authors proposed that dwarfs increase their reproductive investment (to the detriment of growth and maintenance). In this way, dwarfs have a fast growth rate and an early age and reduced size at maturity. They move toward a fast LH strategy (Brown et al. 1993, Raia et al. 2003, Raia and Meiri 2006, Palombo 2007, Meiri and Raia 2010, Larramendi and Palombo 2015). However, the allometric interpretation of insular species does not take in consideration that *r* declines with high densities of populations (*K*) (MacArthur and Wilson 1967), showing evolution of dwarfs in scenarios with unlimited population growth. This problem

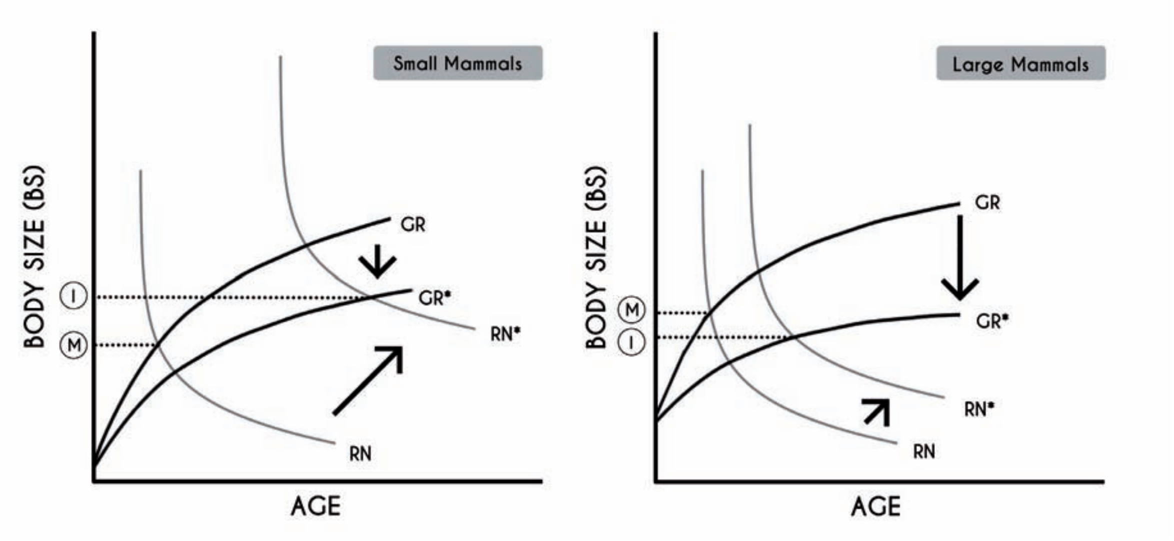

Figure 1.2. Diagrams explaining the shift of adult BS on an island (circled letter I) in relation to that on the mainland (circled letter M), modified from Palkovacs (2003). In order to construct them, it has been taken into account the relative magnitude of shifts in the growth rate curve of the individual (black curves, GR for mainland individual and GR* for island one) and the reaction norm determining age and size at maturity (grey curves, RN for mainland individual and RN* for island one). In the case of small mammals (diagram on the left), the decreased predation rate predominates and, thus, the effect of reduced extrinsic mortality rate (RN to RN*) is greater. In the case of large mammals (diagram on the right), reduced resource availability predominates and, thus, the effect of reduced individual growth rate (GR to GR*) is greater.

remains unresolved and is a controversial issue nowadays. Although the extant populations of insular small mammals have been studied deeply at biological level (Austad 1993, Adler and Levins 1994, Adler 1996, Anderson and Handley 2002, Lambert et al. 2003, White and Searle 2007, Mappes et al. 2008, Salvador and Fernandez 2008a, Barun et al. 2015, Gray et al. 2015, among others), paleontology has focused on the striking dwarfs, and the knowledge of gigantism from this point of view remains widely neglected.

1.2.4. Optimal body size

As a result of this gradual trend, it is observed that the BS of insular extant mammals converges in a range from around 100 to 500 g (Lomolino et al. 2012). Some authors hypothesize that this BS point (where there is no divergence between island dweller and mainland counterparts) would be the "optimal" BS for species. From an energetic point of view, Brown et al. (1993) proposed an optimal BS of 100 g, while Damuth (1993) estimated a value of 1kg. However, the studies of insular dwellers suggested that the optimum varies depending on the bauplan and ecological/thropic strategy of species and characteristics of the island (Maurer et al. 1992, Brown et al. 1993, Marquet and Taper 1998, Lomolino 2005, Lomolino et al. 2012; for contrary view see Raia et al. 2010). In this respect, Maurer et al. (1992) observed that on a gradient of decreasing island surface, maximum BS increases and median BS converges on a hypothetical optimum estimated from the IR for these mammals (Brown et al. 1993). Predictions of the optimal BS are the following: 920 g for all non-volant mammals, 417 g for terrestrial species, 26 g for shrews, 272 g for rodents, 2120 g for rabbits and hares, 6 kg for ungulates and between 83 to 1579 g for carnivores depending on the family (Lomolino 2005, Meiri et al. 2006). However, as Lomolino et al. (2012) said: «*If we were to imagine an unrealistic world in which organisms were not influenced (competed with or preyed upon) by each other, then the optimal size would be microscopic - just large enough to replicate DNA rapidly and with minimal energy. However, interactions among conspecifics and among species are intrinsic and fundamental to natural selection. The optimal size of individuals within a population depends on the size and habits of all others in its community*». In other words, an optimal size does not exist *per se*, it also depends on the habitat (ecosystem) where the organisms live.

Chapter 2

Aims & Objectives

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AIMS & OBJECTIVES

The variation and evolution of BS in islands (IR) has been subjected to numerous studies centered principally on extant faunas (Foster, 1964; Van Valen, 1973a; Heaney 1978; Lomolino 1985, 2005; Lomolino et al., 2012; among others). However, these investigations do not take into account that the current presence of humans and introduced species from the mainland modified this ecogeographical trend. Thus, the extant species do not represent the true natives with whom the research in this field should be done. The fossil record of islands gives us the unique opportunity of working with authentic insular species. The extinct faunas of islands are known for the presence of striking giants, such as *Deinogalerix* sp. or *Nuralagus rex*, and extraordinary dwarfs, such as *Palaeoloxodon falconeri* (Sondaar 1977, Van der Geer et al. 2010). In this way, the studies of BS evolution that deal with extinct species can provide more real and genuine responses for understanding the IR. It has only been recently that several authors have tried to shed light in IR trend and their possible causes analyzing the BM shift of insular extinct mammals (Palombo 2007, 2009a, Lomolino et al. 2013, Van der Geer et al. 2013). The absence of direct values of BS (or BM) of extinct species is the major impediment for researching in this field from a paleontological point of view. Nonetheless, it is widely known that morphometrical traits of the skeleton (teeth or bones) have a close relationship with BM (Damuth and MacFadden 1990a). Statistically, the equations of allometric models allow us to predict the BM of fossil species and gain insights into their biology and ecology. Historically the allometric models for large mammals (primates, elephants, carnivores or ungulates) have prevailed (Damuth and MacFadden 1990a, Christiansen 2004, among others), and, conversely, the models for estimating the weight of orders of small mammals are scarce (Hopkins 2008, Millien and Bovy 2010).

The present PhD Thesis is based on the theoretical framework (exposed in detail along the introduction section) that the special ecological factors of island environments (low predation pressure and interspecific competition, and high intraspecific competition) trigger changes in the LH traits, including BM, of insular dwellers in order to maximize their fitness (MacArthur and Wilson 1967). Thereby, it is predicted that with increasing insularity (smaller and more isolated islands), selection (density-dependent selective regime) encourages the individuals with a greater investment in maintenance and survival (slower life history, *K*-species), at expenses of productivity (*r*-species). Thus, an increase of the age and BS at maturity of small mammals on islands leads to giant morphotypes (Palkovacs 2003). This is a general pattern for insular giants, and biological or phylogenetic factors would play a secondary role, modulating the degree of BS shifts of insular dwellers.

The presented PhD Thesis has the paramount goal of testing this theoretical framework in the fossil register. To this end, Mediterranean Islands were considered the ideal areas of study for several reasons. First of all, the geology and the fossil faunas that dwelled in these islands during the Plio-Quaternary are well known (Alcover et al. 1981, Van der Geer et al. 2010). Some of their remains are stored in *Institut Català de Paleontologia Miquel Crusafont* (ICP), the institution where the dissertation will be developed. Secondly, they are part of a closed system with a narrow latitudinal position (Goffredo and Dubinsky 2014). This allows to remove the variation of BS consequence of the latitude differences (BR) and to focus only on the BS shifts as a result of the insular habitat. Thirdly, the traits of each island are characteristics (differences in the total area, proximity to the mainland, among others) allowing comparisons between them and to delve into the causes and consequences of the ecogeograhical IR trend. The presented PhD Thesis is mainly centered on the study of small mammals. Fossil insular giants were not subject of many scientific studies and the causes and consequences of BS (BM) evolution in this sort of mammals remains widely neglected.

For the previously stated arguments, the presented PhD Thesis has the following specific goals:

I. To perform allometric models for the most represented orders of small mammals in the Mediterranean Islands: Rodentia, Lagomorpha and Soricomorpha (specially the family Soricidae) using data of extant relative species and statistical procedures.

II. To evaluate the best BM proxy for each species (family or order) and predict the BM of certain small insular species from the Mediterranean Islands and their mainland ancestors.

III. To assess whether these species are true giants or not, comparing statistically its BM with that of their ancestors or mainland relatives.

IV. To correlate the BS shifts observed on islands with their ecological contexts (traits of the islands and the faunal complex of each geological moment) in order to seek for evolutionary patterns.

V. To assess the changes in LH traits (and LH strategy) of giant insular species from two perspectives: scaling (BM) and paleohistology.

The following table (Table 2.1, next page) shows an overview of the chapters of this PhD dissertation in relation with the goals proposed.

TABLE 2.1. Schematic chart of the chapters included in the present PhD dissertation, the goals achieved in each of them and the publication to which they refer.

Chapter	Goal achieved	Publication
Chapter 4. How large are the extinct giant insular rodents? New body mass estimations from teeth and bones	I, II and IV	Moncunill-Solé B, Jordana X, Marín-Moratalla N, Moyà-Solà S, Köhler M. 2014. *Integrative Zoology* 9, 197-212. Q1 (Zoology), Impact factor (2014): 1.904
Chapter 5. The Island Rule and the native island of *Mikrotia magna* (Muridae, Rodentia) from the Terre Rose deposits (Gargano, Apulia, Italy): inferences from its body mass estimation	II and IV	Moncunill-Solé B, Jordana X, Köhler M. (To be submitted).
Chapter 6. The weight of fossil leporids and ochotonids: body mass estimation models for the order Lagomorpha	I and II	Moncunill-Solé B, Quintana J, Jordana X, Engelbrektsson P, Köhler M. 2015. *Journal of Zoology* 295, 269-279. Q1 (Zoology), Impact factor (2014): 1.883
Chapter 7. Comparing the body mass variations in endemic insular species of the genus *Prolagus* (Ochotonidae, Lagomorpha) in the Pleistocene of Sardinia (Italy)	II, III and IV	Moncunill-Solé B, Tuveri C, Arca M, Angelone C. 2016. *Rivista Italiana di Paleontologia e Stratigrafia* 122, 25-36. Q3 (Paleontology), Impact factor (2014): 0.938
Chapter 8. First approach of the life history of *Prolagus apricenicus* (Ochotonidae, Lagomorpha) from Terre Rosse sites (Gargano, Italy) using body mass estimation and paleohistological analysis	II, III and V	Moncunill-Solé B, Orlandi-Oliveras G, Jordana X, Rook L, Köhler M. 2016. *Comptes Rendus Palevol* 15, 235-245. Q2 (Paleontology), Impact factor (2014): 1.192
Chapter 9. How common is gigantism in insular fossil shrews? Examining the "Island Rule" in soricids (Mammalia: Soricomorpha) from Mediterranean Islands using new body mass estimation models	I, II, III and IV	Moncunill-Solé B, Jordana X, Köhler M. 2016. *Zoological Journal of the Linnean Society*, Online. Q1 (Zoology), Impact factor (2014): 2.717

Columns: Chapter (number and title), Goals achieved (in this chapter) and Publication (authors, year, journal, number, pages, quartile and impact factor).

Chapter 3

Materials & Methods

MATERIALS & METHODS

3.1. Database of extant and extinct fauna

The material used in the present PhD Thesis can be divided into two clusters: 1) extant: material of current species used for performing the BM predictive models; and 2) extinct: material of fossil species used for estimating their BM and making inference on the selection pressures behind the IR. In both groups, only adult specimens (those with fused epiphyses) were used.

The extant analyzed material includes a total of 1340 individuals from 170 species belonging to three different orders: Rodentia, Lagomorpha and Soricomorpha (58, 48 and 64 species respectively) (Table 3.1). The collection of rodents comes from the Rijksmuseum van Natuurlijke Historie (RMNH), the Universitat de Barcelona (UB), the Universitat de les Illes Balears (UIB), and the Museo de Ciencias Naturales de Madrid (MCNM). In respect to lagomorphs, it is housed in the Smithsonian Institution National Museum of Natural History (SINMNH), and the material of soricids is stored in the Magyar Természettudományi Múzeum (NHMUS). The analyzed material of fossil species comprises a total of 2250 individuals from 22 species belonging to the three orders under study (6 rodent species, 5 species of lagomorphs, and 11 species of soricids) (Table 3.2). The fossil material includes species that inhabited mainland and islands (Canary and Mediterranean Islands) ranging from Miocene to Holocene. Data of some of the analyzed species was collected from specimens stored in Institut Català de Paleontologia Miquel Crusafont (ICP) (*Canariomys bravoi* Crusafont-Pairó and Petter 1964; *Hypnomys morpheus* Bate 1918; *Hypnomys onicensis* Reumer 1994; *Muscardinus cyclopeus* Agustí, Moyà-Solà and Pons-Moyà 1982; and *Prolagus* cf. *calpensis* Major 1905), in the Università degli Studi di Firenze (UNIFI) (*Mikrotia magna* (Freudenthal 1976) from several sites, and *Prolagus apricenicus* Mazza 1987 from several sites) and in the Soprintendenza dei Beni Archeologici per le Province di Sassari and Nuoro (SSN) (*Prolagus figaro* López-Martínez 1975 from several sites, and *Prolagus sardus* from several sites). For other species, data from the literature was used to perform the analyses (*Canariomys tamarani* López-Martínez and López-Jurado 1987; *Nuralagus rex*; *Asoriculus burgioi* Masini and Sarà 1998; *Asoriculus gibberodon* (Petényi 1864); *Asoriculus similis* (Hensel 1855); *Crocidura kornfeldi* Kormos 1934; *Crocidura sicula esuae* (Kotsakis 1986); *Crocidura sicula sicula* (Miller 1901), *Crocidura zimmermanni* Wettstein 1953; *Nesiotites ponsi* Reumer 1979; *Nesiotites* aff. *ponsi*; *Nesiotites meloussae* Pons-Moyà and Moyà-Solà 1980; and *Nesiotites hidalgo* Bate 1945). For further details of the materials, see the specific chapter (chapters 4 and 5 for Rodentia, chapters 6, 7 and 8 for Lagomorpha and chapter 9 for Soricomorpha).

In order to analyze the IR from a paleontological point of view, it is very important to know the FCs and ecosystems that were present on the islands in different geological periods. For this reason, previously, a bibliographic compilation of the species that dwelled in Mediterranean Islands, the principal zone subjected under study, were done. This compilation is presented in form of supplementary data of this chapter (section 3.4). It includes the period of FCs, the species and families observed, the probable ancestor, the diet and other information of the species. This information allows us to know precisely the fauna and assess and compare the ecological pressures of different islands.

Table 3.1. Material of current species used in the present PhD dissertation for carrying out the BM predictive models.

Order	Family	Genus	Nº of species				Nº of individuals
			Total	Teeth	Skull	Postcranial	Total
Rodentia	Bathyergidae	Several	2 species	2	2	1	22
	Capromyidae	Several	3 species	2	3	2	3
	Castoridae	*Castor*	1 species	1	1	1	6
	Caviidae	Several	5 species	5	5	4	20
	Cricetidae	Several	5 species	3	5	5	69
	Dasyproctidae	Several	3 species	3	3	2	30
	Dipodidae	*Jaculus*	1 species	1	1	1	11
	Geomyidae	*Geomys*	3 species	3	3	0	10
	Gliridae	Several	2 species	2	2	1	77
	Hystricidae	*Hystrix*	1 species	1	1	1	4
	Muridae	Several	20 species	17	20	7	203
	Nesomyidae	Several	2 species	2	2	1	3
	Pedetidae	*Pedetes*	1 species	1	1	1	7
	Sciuridae	Several	7 species	7	7	5	58
	Spalacidae	*Rhizomys*	1 species	1	1	1	12
	Thryomyidae	*Thryonomys*	1 species	1	1	1	4
			58 species	**52**	**58**	**34**	**539**
Lagomorpha	Ochotonidae	*Ochotona*	12 species	12	12	12	119
	Leporidae	Several	36 species	30	23	36	318
			48 species	**42**	**35**	**48**	**437**
Soricomorpha	Soricidae	*Anourosorex*	2 species	2	0	2	3
		Blarina	1 species	1	0	1	5
		Chimarrogale	1 species	1	0	0	1
		Crocidura	30 species	30	3	12	201
		Cryptotis	1 species	1	0	0	3
		Diplomesodon	1 species	0	0	1	1
		Episoriculus	2 species	2	0	2	13
		Neomys	2 species	2	0	2	29
		Notiosorex	1 species	1	0	1	1
		Sorex	20 species	20	2	7	88
		Soriculus	1 species	1	0	1	9
		Suncus	2 species	2	0	2	10
			64 species	**63**	**5**	**31**	**364**
TOTAL OF EXTANT MATERIAL			170 species	157	98	113	1340

Columns: order, family, genus (the name of the genus or "several" when the family includes more than one), nº of species analyzed (total, for teeth models, for skull models, and for postcranial models) and total nº of individuals. For further details, see the specific chapter (chapter 4 for Rodentia, chapter 6 for Lagomorpha and chapter 9 for Soricomorpha).

TABLE 3.2. Material of extinct species used in the present PhD dissertation for predicting their BM.

Order	Family	Species	Site	Chronology	Nº of individuals				Literature/ Institution
					Total	Teeth	Skull	Postcranial	
Rodentia	Muridae	*Canariomys bravoi*	Cueva de las Palomas (Tenerife, Spain)	Holocene	280	74	11	195	ICP
	Muridae	*Canariomys tamarani*	La Aldea (Gran Canaria, Spain)	Holocene	17	0	0	17	López-Martínez and López-Jurado (1987)
	Muridae	*Mikrotia magna*	Several fissures: F8, F9 and San Giovannino (Gargano, Italy)	Late Miocene	82	0	0	82	UNIFI
	Gliridae	*Hypnomys morpheus*	Cova de Sa Bassa Blanca (Mallorca, Spain)	Holocene	203	74	0	129	ICP
	Gliridae	*Hypnomys onicensis*	Sa Pedrera de s'Ònix (Mallorca, Spain)	Late Pliocene	261	10	0	251	ICP
	Gliridae	*Muscardinus cyclopeus*	Punta Nati-3 (Menorca, Spain)	Pliocene	48	28	0	20	ICP
					891	**186**	**11**	**694**	
Lagomorpha	Ochotonidae	*Prolagus apricenicus*	Several sites: F1 and F8 (Gargano, Italy)	Late Miocene	85	18	0	67	UNIFI
	Ochotonidae	*Prolagus* cf. *calpensis*	Casablanca I (Almenara, Spain)	Late Pliocene	133	29	0	104	ICP
	Ochotonidae	*Prolagus figaro*	Several sites: X3, IVm and X4 (Monte Tuttavista, Sardinia, Italy)	Late Pliocene - Early Pleistocene	59	0	0	59	SSN
	Ochotonidae	*Prolagus sardus*	Several sites: XIr and VI6 (Monte Tuttavista, Sardinia, Italy)	Middle - Late Pleistocene	254	0	0	254	SSN
	Leporidae	*Nuralagus rex*	Punta Nati-6 (Menorca, Spain)	Early Pliocene	113	20	0	93	Quintana Cardona (2005)
					644	**67**	**0**	**577**	
Soricomorpha	Soricidae	*Asoriculus burgoi*	Monte Pelegrino (Sicily, Italy)	Early Pleistocene	1	1	0	0	Masini and Sarà (1998)

	Soricidae	*Asoriculus gibberodon*	Sima del Elefante (Atapuerca, Spain)	Early Pleistocene	8	8	0	0	Rofes and Cuenca-Bescós (2006)
	Soricidae	*Asoriculus similis*	Sardinia, Italy	Late Pleistocene	3	3	0	0	Rofes et al. (2012)
	Soricidae	*Crocidura kornfeldi*	Sima del Elefante (Atapuerca, Spain)	Late Pliocene	109	109	0	0	Rofes and Cuenca-Bescós (2011)
	Soricidae	*Crocidura sicula esuae*	Isolidda 3 - US 13 (Sicily, Italy)	Middle Pleistocene	153	153	0	0	Locatelli (2010)
	Soricidae	*Crocidura sicula sicula*	Oriente Cave (Sicily, Italy)	Late Pleistocene - Holocene	19	19	0	0	Locatelli (2010)
	Soricidae	*Crocidura zimmermanni*	Several sites: Xeros, Stavros-Micro, Stavros-Cave, Milatos 2, Rethymnon fissure, Liko a, Liko A, Liko B, Liko C, Liko D and Recent diposits (Crete, Greece)	Pleistocene - Holocene	402	402	0	0	Reumer (1986)
	Soricidae	*Nesiotites ponsi*	Cruis de Cap Farrutx (Mallorca, Spain)	Late Pliocene	4	4	0	0	Rofes et al. (2012)
	Soricidae	*Nesiotites* aff. *ponsi*	Pedrera de s'Ònix (Mallorca, Spain)	Early Pleistocene	6	6	0	0	Rofes et al. (2012)
	Soricidae	*Nesiotites meloussae*	Barranc de Binigaus (Menorca, Spain)	Early Pleistocene	1	1	0	0	Rofes et al. (2012)
	Soricidae	*Nesiotites hidalgo*	Several sites: Cova de Llenaire, Cova Estreta and Cova de Canet (Mallorca, Spain)	Late Pleistocene - Holocene	9	9	0	0	Rofes et al. (2012)
					715	715	0	0	
TOTAL OF EXTINCT MATERIAL					2250	968	11	1271	

Columns: order, family, species, site, chronology, nº of analyzed individuals (total, for teeth models, for skull models and for postcranial models), and literature (reference where appropriate)/institution (of storing). For further details, see the specific chapter (chapters 4 and 5 for Rodentia, chapters 6, 7 and 8 for Lagomorpha, and chapter 9 for Soricomorpha).

3.2. Skeletal measurements and body mass data

For each individual (extinct and extant), a set of measurements on teeth, skull and long bones (principally femora, humerus and tibia; but in rodents the cubit/ulna and pelvic bone were also studied) were taken. For this task, a digital electronic precision caliper (0.05 mm error) and a measuroscope (Nikkon Measuroscope 10) were used.

Table 3.3. Descriptions and abbreviations of the measurements taken on skeletal elements.

Skeletal element	Measurement description	Abbreviation	Figure		
			Rodentia	Lagomorpha	Soricidae
Teeth	Length of the lower first molar	LM/1	3.1 A	3.1 B	*3.1 C1
Teeth	Width of the lower first molar	WM/1	3.1 A	3.1 B	*3.1 C1
Teeth	Lower molar tooth row length	TRL or TRLM/1	-	3.3 B	3.4 B
Teeth	Area of the lower first molar	AAM/1	*3.1 A	*3.1 B	*3.1 C1
Teeth	Area of the lower molar tooth row	TRAAM/1	-	*3.1 B and 3.3 B	*3.1 C1 and 3.4 B
Teeth	Length of the upper first molar	LM1/	X	X	3.1 C2
Teeth	Width of the upper first molar	WM1/	X	X	*3.1 C2
Teeth	Upper molar tooth row length	TRLM1/	X	X	-
Teeth	Area of the upper first molar	AAM1/	X	X	*3.1 C2
Teeth	Area of the upper molar tooth row	TRAAM1/	X	X	-
Skull	Width of occipital condyles	WOC	-	3.3 A	3.4 A
Femur	Femur length	FL	3.2 A	3.3 C	3.4 C
Femur	Proximal femoral transversal diameter	FTDp	3.2 A	3.3 C	3.4 C
Femur	Distal femoral anteroposterior diameter	FAPDd	3.2 A	3.3 C	3.4 C
Femur	Distal femoral transversal diameter	FTDd	3.2 A	3.3 C	3.4 C
Humerus	Humerus length	HL	3.2 B	3.3 D	3.4 D
Humerus	Proximal humeral anteroposterior diameter	HAPDp	3.2 B	3.3 D	3.4 D
Humerus	Distal humeral anteroposterior diameter	HAPDd	3.2 B	3.3 D	3.4 D
Humerus	Distal humeral transversal diameter	HTDd	3.2 B	3.3 D	3.4 D
Tibia	Tibia length	TL	3.2 E	3.3 E	3.4 E
Tibia	Proximal tibia anteroposterior diameter	TAPDp	3.2 E	3.3 E	3.4 E
Tibia	Proximal tibia transversal diameter	TTDp	3.2 E	3.3 E	3.4 E
Tibia	Distal tibia transversal diameter	TTDd	3.2 E	3.3 E	3.4 E
Pelvic bone	Pelvic bone length	PL	3.2 C	X	X
Cubit/Ulna	Cubit/Ulna length	CL	3.2 D	X	X

Columns: skeletal element (teeth, skull, femora, humerus, tibia, pelvic bone or cubit/ulna), measurement description, abbreviation and figure (number and letter of figure, dash when no figure is given, cross when this measurement is not taken in this order and asterisk when the figure indicate other measurements that are needed for calculating it). For further details of measurements, see the specific chapter (chapter 4 for Rodentia, chapter 6 for Lagomorpha and chapter 9 for Soricomorpha).

The measurements are the same for the three different orders. Regarding teeth, it is taken the length and width of the lower first molar (LM/1 and WM/1) and the lower molar tooth row length (TRL or TRLM/1). Area of the molar (AAM/1, product of the length and width) and area of the tooth row (TRAAM/1, product of the molar tooth row length and width) were subsequently calculated (Table 3.3). Exceptionally in the case of soricids, these measurements were also taken in the upper dentition (LM1/, WM1/, and TRLM1/, AAM1/, and TRAAM1/) (Table 3.3). Only one measurement, the width of occipital condyles (WOC), was taken in the skull (Table 3.3). In the case of postcranial material, it is measured the total length of the bone and the anteroposterior and transversal diameters of epiphyses. The description of postcranial measurement and its abbreviation are in Table 3.3. All these

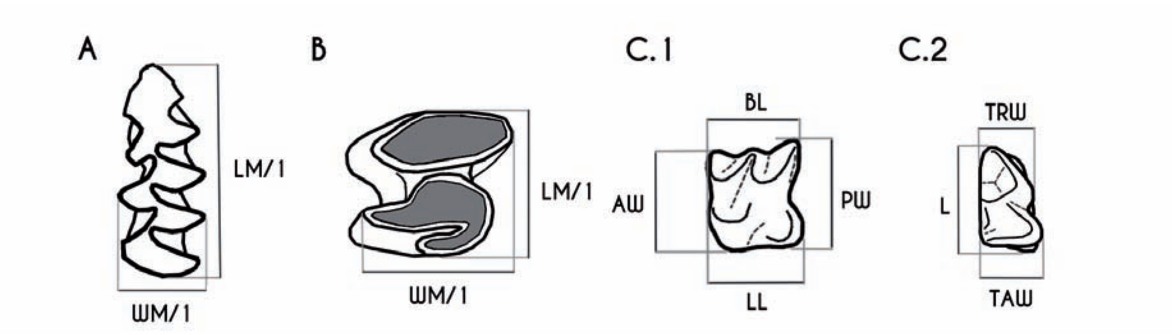


Figure 3.1. Measurements taken on first molars of the mammal orders assessed: A) Order Rodentia (it is represented by a teeth of *Arvicola* Lacépède 1799): lower first molar, B) Order Lagomorpha (it is represented by a teeth of *Eurolagus* López-Martínez 1977): lower first molar, and C) Family Soricidae: upper (1) and lower (2) first molar. Abbreviations of rodents and lagomorphs are described in the text and in Table 3.3. For soricids, the measurements of Reumer (1984) were averaged (see chapter 9 for further explanations and abbreviations). Items A and B are drawn by the author. Items C are modified from Reumer (1984).

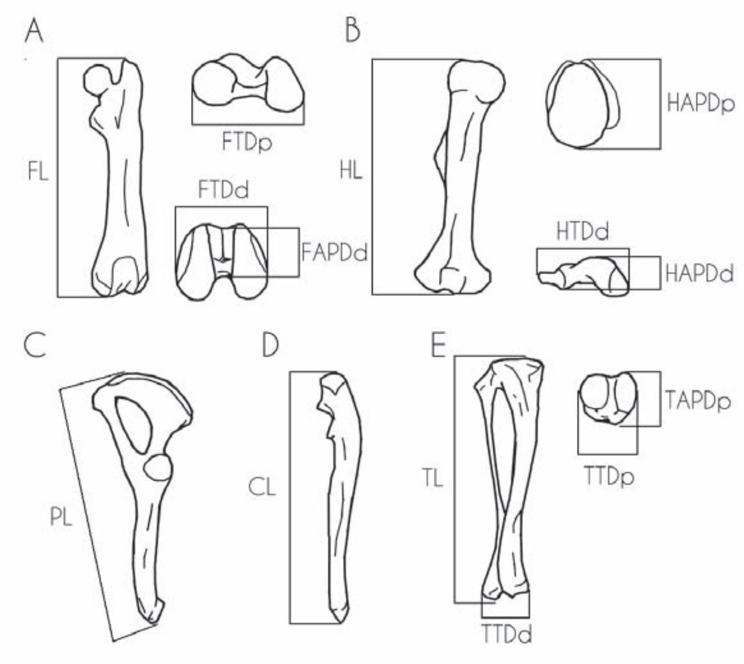


Figure 3.2. Measurements of the postcranial bones for the order Rodentia. A) Femur; B) Humerus; C) Pelvic bone; D) Cubit/Ulna; and E) Tibia. Abbreviations are described in Table 3.3. Figure modified from Cabrera (1980).

measurements were described in Cabrera (1980), Reumer (1984), Köhler and Moyà-Solà (2004), Blanco (2005), Quintana Cardona (2005) and Hopkins (2008). Considering the postcranial bones of soricids, the measurements were adapted to its particular morphology taking into account those of rodents and lagomorphs. For more details, see the specific chapter or Figure 3.1, 3.2, 3.3 and 3.4.

In some cases, the BM of extant specimens was recorded in the collections. Although it is preferable the real value of the specimen that is measured, when it was not specified in the collections, the data was gathered from the published literature (Silva and Downing 1995, among others). Small mammals, the principal subjects of this PhD Thesis, do not show significant sexual BS differences (Lu et al. 2014). Thus, data of males and females were not analyzed separately.

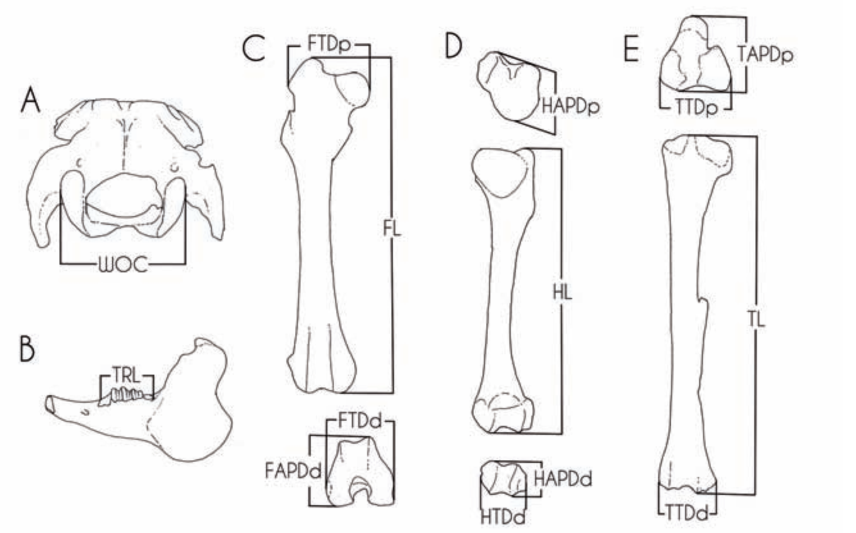


Figure 3.3. Measurements of the skull and postcranial bones for the order Lagomorpha. A) Skull; B) Mandible; C) Femur; D) Humerus; and E) Tibia. Abbreviations are described in the text and in Table 3.3. Figure modified from Quintana Cardona (2005).

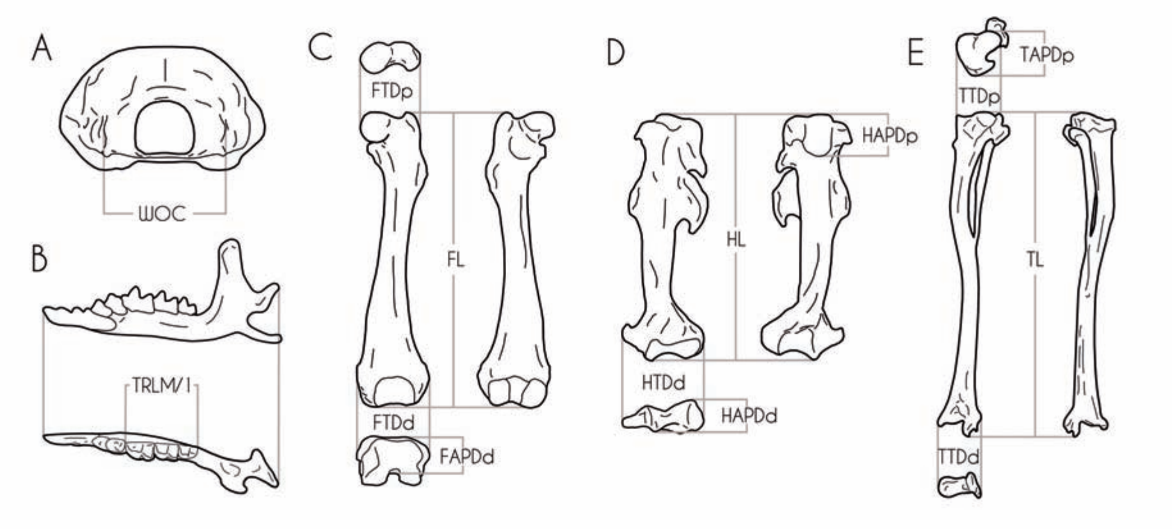


Figure 3.4. Measurements of the skull and postcranial bones for the family Soricidae (Order Soricomorpha). A) Skull; B) Mandible; C) Femur; D) Humerus; and E) Tibia. Abbreviations are described in the text and in Table 3.3. Figure drawn by the author.

3.3. Statistical methodology

Allometry for predicting body mass

The allometric relationships are usually represented as power formulae: $Y = Y_0X^b$; where Y is some dependent variable, Y_0 is a normalized constant (also known as a), X is the independent variable, and b is the scaling exponent. When the main objective is to reconstruct the weight of extinct species, the response variable (Y) is the BM, and the controlled variable (X) is one or more morphological traits (measurements of teeth or bones). This quantitative relationship is established using extant representative species and then is applied for predicting the BM of extinct ones (Peters 1983, Schmidt-Nielsen 1984). In this process, several considerations need to be taken into account in advance when seeking allometric models for predicting BM:

Firstly, the choice of reference data for constructing the allometric regression and predicting the BM in extinct species is critical (Peters 1983, Reynolds 2002, Millien and Bovy 2010). The allometric relation between the skeletal trait (teeth, cranium or postcranial bones) and BM have to be the same for extinct species and living species used in the model. In other words, the species used for constructing the model (extant) and those used for predicting their BM (extinct) have to be analogs (Reynolds 2002). Consequently, the reference data is usually related to extinct species phylogenetically, functionally or both (Bryant and Russell 1992). The use of allometric equations to predict the BM of extinct species that lie taxonomically or adaptively far outside the reference data (those species used to perform the model) is unrealistic biologically. In contrast, some authors prefer wider taxonomic sets, including not only the immediate related species (Roth 1990). They select extant species based more on a criterion of adaptive similarity (Schwartz et al. 1995). A broader comparative study is suggested to have a larger potential of capturing most of the essential features of interest when extinct species do not have many extant relatives (Reynolds 2002), especially in multiple models (Mendoza et al. 2006). On the other hand, the use of species related phylogenetically restricted the statistical methodologies, because they are not "cases" statistically independent among them (Harvey and Pagel 1991). However, in order to subtract the effect of phylogeny is necessary to know the phylogenetic relationships of extant species. This is difficult, sometimes impossible, when working with large sample sizes (N), especially in small mammals where the phylogenetic relationships among species are not clear.

Secondly, the N is paramount and should be large enough to allow as much confidence as possible in the predictions and cover the larger range of BS possible. The extinct species values have to fall within the range of reference data (living species) avoiding the extrapolation of results beyond the model (Schmidt-Nielsen 1984, Damuth and MacFadden 1990b, Zar 1999, Reynolds 2002).

Thirdly, particularly relevant is also the choice of the skeletal traits used for estimating BM (Reynolds 2002, Millien and Bovy 2010). The most used measurements are from teeth (length, width or area, particularly of the lower first molar) and cranium, for their easy determination and high abundance in the fossil record (Reynolds 2002, Hopkins 2008). Conversely, postcranial bones are involved in the weight bearing. Because of the different functional constraints of teeth and postcranial bones, their BM predictions might not be in agreement (Millien and Bovy 2010). Diameters and perimeters of long bones are usually better predictors than length, and zeugopods, involved in the locomotion and preferences of the animal, are less related with BM generally (Scott 1990, Millien and Bovy 2010).

Fourthly, the intraspecific variability is not considered because the allometric relation is looked at higher taxonomic levels, in our case at the level of order or family. Thus, the reference data have to be composed only of interspecific data (Millen and Bovy 2010). For this reason, in all the analyses performed in this PhD Thesis, the average of multiple individuals was used to carry out the model.

Sometimes, these set of considerations would be difficult to achieve. The fossil species may not have close living relatives with which to make the comparisons (e.g. dinosaurs) (Reynolds 2002) or closer sister taxa may not show the same allometric relationship among the BM and morphological trait (Janis 1990). The fossil mammals analyzed in this PhD Thesis have extant sister taxa for carrying out the regression analyses. The maximum taxonomic diversity is included for getting broad BM range. This is appropriate for BM estimations to avoid extrapolation far away from the model. Furthermore, taking into account a high taxonomic diversity, the effects of phylogeny are minimized.

Statistical regression models: Ordinary Least Squares

The statistical method of least-squares (Ordinary Least Squares, OLS, Model I) is the most common approach to regression in biology and allometry for fitting the data (Peters 1983), although other techniques and methodologies exist (Reduced Major Axis, RMA, Model II). The objective of the regression methodology is to find the line (allometric equation) that, on average, describes the available data with the smallest errors. When the principal use of the relationship is the prediction, it is recommended the use of OLS instead of RMA. Reporting the slope (b) and intercept (Y_0 or a) is sufficient for predicting mean values for the dependent variable (BM) (Quinn and Keough 2002). However, one of the main important limitations of OLS is its sensitivity to extreme values which can carry out a misleading relationship between parameters. Thus, it is preferable that the data is spread homogenously along all the range of the independent variable (Peters 1983). The analyses were performed using the IBM SPPS Statistics 19 software [Property of SPPS, Inc. (Chicago, USA), and IBM Company (Armonk, USA)].

To improve the diagrammatic, statistical descriptions and interpretation of allometric relationships, the values of variables (BM and skeletal measurements) are transformed to logarithms in advance of performing the analysis. Thus, the power function ($Y = Y_0X^b$) turns to a straight line ($\log Y = \log Y_0 + b\log X$) (Peters 1983, Schmidt-Nielsen 1984). Two types of regression models were conducted: 1) bivariate or simple, and 2) multiple. The simple regression models are those that relate the BM with only one skeletal measurement. The formula obtained for the prediction has the form of $\log BM = \log Y_0 + b\log X$. On the other hand, the multiple models are those that relate the BM with more than one skeletal measurement. The formula of these relationships follows $\log BM = \log Y_0 + b_1\log X_1 + b_2\log X_2 + b_3\log X_3 + \ldots + b_k\log X_k$; where k is the total number of selected traits that are related with BM (Quinn and Keough 2002). The stepwise selection of predictor variables is used when multiple models were performed. In this case, the predictors are entered into the multiple regression equation one at a time based upon statistical criteria (specific size of partial F statistics with significance levels greater than 0.05), starting with those that contributes the most to prediction equation (in terms of increasing the multiple correlation). This process is continued only if additional variables add anything statistically to the regression equation. In the case that this does not occur, the analysis stops with the variables introduced (Quinn and Keough 2002). This avoids redundant information and working with a lower number of variables.

Exceptionally in the case of order Rodentia (chapter 4), the data was also converted into cubic and square roots, depending on category of the measurement (volume or area respectively), before to perform the model for the purpose of scaling the results. However, over the years of PhD Thesis, it is observed that this procedure does not improve the results, but it may introduce errors in the transformation of the values. For this reason, this data conversion was only used in the first studies of the PhD Thesis.

Assessment of the regression models

Generally, no single observation will fall exactly on the allometric regression line performed, but the deviation from the line can be of small or large importance (Schmidt-Nielsen 1984). Those values remote from the regression equation in a significant way are coined as outliers. They can lead to substantial distortions of the parameters and statistic estimates and the outcome and accuracy of regression model is affected. In order to detect them, the Cook's distance ($D_i = \frac{\sum_{j=1}^{N}(\hat{Y}_j - \hat{Y}_{j(i)})^2}{p\,MSE}$ where $\hat{Y}_j$ is the prediction from the full regression model for observation *j*, $\hat{Y}_{j(i)}$ is the prediction for observation *j* from a refitted regression model in which observation *i* has been omitted, *p* is the number of fitted parameters in the models, and *MSE* is the mean square of the regression model) is used. Values with a D_i greater than 1 are of particular influence and it is preferable their elimination (Quinn and Keough 2002) (Table 3.4). Of importance is also the distribution of these deviations (residues) in order to observe if they are scattered homogeneously independent of the value of predictor variable. A positively or negatively skewed distribution is indicative that the model does not have the same prediction power for all the range of the *Y* variable and, probably, other type of functions, instead of the linear one, can explain better the variability. In this case, the homogeneity of residues was controlled through residual plots (predicted *Y* vs. residuals). The ideal plot is a scatter of points without an obvious pattern of increasing or decreasing variance in the residuals. If this requirement is not met, the regression model is considered invalid (Quinn and Keough 2002).

Table 3.4. Descriptions and abbreviations of the statistical measurements used.

Statistical parameter	Abbreviation	Definition	Literature
Cook's distance	D_i	It is indicative of the influence of each observation on the fitted response values. It is useful for identifying outliers	Quinn and Keough (2002)
Coefficient of determination	r^2	It is indicative of the goodness of fit of the regression models	Smith (1980)
Standard error of the estimate	SEE	It is indicative of the accuracy of the predictions	Quinn and Keough (2002)
Average absolute percent prediction error	%PE	It is indicative of the deviation of the observed values from their predictions by the regression equation	Smith (1984)
Mean absolute percent prediction error	MAPE	It expresses the accuracy as a percentage of the error	Schaeffer (1980)
Ratio Estimator	RE	Correction factor. It is the ratio of means of two variables	Snowdon (1991)

Columns: Statistical parameter, Abbreviation, Definition, and Literature.

Allometric equations are accompanied by statistical values that reflect the accuracy, precision and adjustment of each model and allow the comparison among different models (Smith 1980, 1984, Quinn and Keough 2002) (Table 3.4). It is calculated the coefficient of determination (r^2), the standard error of the estimate (SEE), and the average absolute percent prediction error (%PE). The r^2 is a useful index to test the goodness of fit of the regression model. It ranges from a value of 1, indicating that the regression model explains all the variation; to 0, when none variation is explained by the model. However, it is highly affected by the total sample used and the range of values of the dependent variable, showing significant results (high value of r^2) when there are also high deviations (residues) (Smith 1980). The SEE is a measure of the accuracy of predictions and is calculated as the standard deviation of the errors of prediction. Low values of SEE are indicative that the observations tend to cluster more closely around the prediction line and, in other words, that the model is more accurate. The %PE is calculated following the formula %PE=[(observed-predicted)/predicted*100] proposed by Smith (1984). The value of %PE is an indication of the average percentile deviation of the observed points from the values predicted by the regression equation. In the same way as SEE, low values of %PE are indicating more precision of the model. The mean absolute percent prediction error (MAPE) informs us about the accuracy of the model and is very similar to the %PE. Due to this, MAPE ($=\frac{100}{\mathrm{N}}\sum_{t=1}^{N}|(y_t - \hat{y}_t/y_t|)$) was only calculated in the regression models of rodents. However, in last instance, choosing the best estimator model of BM for an extinct species does not only depend on the accuracy of the models, but also in a subjective judgment of the results of predictions (Reynolds 2002). In the Table 3.4, there is a brief summary of these statistical parameters and their meaning.

In order to test the resultant equations of the regression models, we performed leave-one-out cross-validation tests (LOOCVs) (Geisser 1975). For each species a new equation was carried out without the species' data concerned. This new equation is used for predicting the BM of this species. The process was repeated for all the species. Thus, we obtained predicted (from the equation without the species' data) and observed (real) values for each species. Correlations (r) between these values (predicted and observed scores) and the cross-validation error informed us about the suitability of the equations.

The specialized skeletal adaptations of forelimbs and hindlimbs (reflecting positional behavior and locomotion) and the specific teeth morphology of some groups (reflection of the diet) can bring background noise to the regression models (Reynolds 2002). Sometimes, deviations (outliers) observed from the line equations may be indicative of secondary signals. Thus, some groups would have predictable deviations from the general allometric relationship (Schmidt-Nielsen 1984). When this could happen, the data was split by groups (locomotion, diet, phylogeny or others) and different regression models were carried out. The statistical differences among these split models (equations) were tested with an analysis of covariance (ANCOVA) (significance $p < 0.05$). Only when there were significant differences, the equations were presented (Quinn and Keough 2002).

Predicting the body mass of fossil species

The use of logarithm of observations for performing the regression models introduces an error when the predicted values are transformed to the original observable units (Smith 1993). In order to correct this, it is used the Ratio Estimator (RE). RE, calculated for each regression model, is the result of $\bar{y}/\bar{z}$, where y_i is the observed value of the dependent variable y for the ith observation on the original measurement scale and z_i is the predicted value for the ith observation, detranformed back to the original measurement scale without correction (Snowdon 1991, Smith 1993). This correction factor (RE) is multiplied by the detransformed predicted values (values of BM) of each equation.

For each specific measurement, the BM of species and the confidence interval (IC=$\bar{x}\pm\frac{\sigma}{\sqrt{N}}Z_{\sigma/2}$) is obtained averaging the estimated BM of each individual. Based on the BM of each measurement, it is possible to calculate a simply average ($\bar{x}$), a geometric mean ($\bar{x}_G$), and a weighted mean ($W_M= \sum_{Mi}^{1}((\frac{Mi}{\%PE} \text{ x } \sum_{Mi}^{1} \%PE) \text{ x } N^{-2})$) for the species (Scott 1990, Christiansen and Harris 2005, Mendoza et al. 2006). The use of one kind of average or other depends of the sample type. For example, in the cases where there is a large difference of number of individuals for measurements, it is important to assess the $\bar{x}_G$. On the other hand, in the cases when we estimate the BM with several regression equations highly different in their %PE, it is interesting to calculate the W_M. To test the BM differences statistically between ancestor and insular species or anagenetic species series, parametric (T-test and ANOVA analyses) or non-parametric tests (Mann-Whitney and Kruskal-Wallis analyses) were performed, as appropriate for the sample (significance $p < 0.05$) (Schwartz et al. 1995).

3.4. Supplementary data

The following tables are the bibliographic compilation of the FCs observed on the most important Mediterranean Islands from Pliocene to Holocene period (excepting Gargano, where only fauna of Miocene is known, and Sardinia, where the FC of *Oreopithecus bambolii* Gervais 1872 from Late Miocene is also included) (Fig. 3.5). Islands are organized by alphabetic order, excepting Sicily and Malta as a result of their similar FCs. Sardinia and Corsica are considered together because they are connected during the Quaternary Period. They are codified as: 1) Crete, 2) Cyprus, 3) Gargano, 4) Gymnesic Islands, 5) Sardinia and Corsica, 6) Sicily, 7) Malta, 8) Pityusic Islands, and 9) Small islands (Fig. 3.5). Columns: Faunal Complex (in some cases, the FC has not a particular name), Geological age, Order, Family, Species, Ancestor, Diet (C, Carnivore; I, Insectivore; H, Herbivore; HFO, Folivore; HFR, Frugivore; HGR, Gramnivore; O, Omnivore; and N, Necrophagous/ Scavenger) and More Information (additional information of the BS, ancestor, origin, among other traits). Abbreviations used in the Order column: A, Artiodactyla; C, Carnivora; I, Insectivora; L, Lagomorpha; P, Perissodactyla; PI, Primates; PR, Proboscidea; Q, Chiroptera; and R, Rodentia. In Diet column: the symbol “X” is used to indicated that the diet of this species is described in the bibliography, and the symbol “?” when we deduced the diet according to its mammalian order. Abbreviations used in the HFO column: B, browser; G, grazer; and MF, mixed feeder. Information of FCs is based on Sondaar and Boekschoten (1967), Freudenthal (1971), Alcover et al. (1981), Petronio (1990), Hunt and Schembri (1999), Bonfiglio et al. (2002), Marra (2005, 2013), Sondaar and Van der Geer (2005), Palombo (2006, 2007, 2009b), Raia and Meiri (2006), Theodorou et al. (2007), Bover et al. (2008), Masini et al. (2008, 2010), Masseti (2009), Lyras et al. (2010), Van der Geer et al. (2010), and particular references on each table. Feeding information is based on Raia and Meiri (2006), Palombo (2009a, 2009b), Van der Geer et al. (2010), Jordana et al. (2012), Marra (2013) and Rozzi (2013).

FIGURE 3.5. Diagram of the Mediterranean Sea and its Islands: 1) Crete, 2) Cyprus, 3) Gargano (paleo-island), 4) Gymnesic Islands, 5) Sardinia and Corsica, 6) Sicily, 7) Malta, 8) Pityusic Islands, and 9) some Small Islands.

1. CRETE

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
Kritimys Zone FC Archipelago, oceanic-like island of type 2 (1). High endemic, low biodiversity, impoverished and unbalanced. Micromammals probably arrived by sweepstake route. The large mammals present are good swimmers. Previously it was submerged until Early Pleistocene. Sites: Siteia 1, Cape Maleka 1, Katharo 1, among others	Early to Middle Pleistocene. Subdivided in two biozones: *K. kiridus* (Early Pleistocene) and *K. catreus* (Early-Middle Pleistocene)	R	Muridae	*Kritimys* aff. *kiridus*	*Praomys* (2)							?		Literature: 1, 2, 3, 4, 5, 6. Endemic. Anagenetic lineage: *K.* aff. *kiridus* > *K.kiridus* > *K.catreu* (3). They are not found together. Probably migration from Rhodes (3). Increase in BS over time
		R	Muridae	*Kritimys kiridus*								?		
		R	Muridae	*Kritimys catreus*								?		
		I	Soricidae	*Crocidura zimmermanni*	*C. kornfeldi* (3)		?							Literature: 3, 4, 6. *K. catreus* bizone: only in the youngest sites of this zone (Xeros)
		A	Hippopotamidae	*Hippopotamus creutzburgi*	*H. antiquus* (1,3)				MF/ G					Literature: 1, 2, 3, 4, 5, 6. *K. catreus* bizone. Two subspecies: *H. creutzburgi creutzburgi* (older sites), and *H. creutzburgi parvus* (younger sites) (3). Endemic, small BS. It is adapted for walking and running (2,3)
		PR	Elephantidae	*Mammuthus creticus*	*M. meridionalis* (1,3)				?B					Literature: 1, 2, 3, 4, 5, 6. = *Elephas creticus* or *E. cretica* (7,8). *K. kiridus* bizone. Endemic. Dwarf
The fauna of the previous FC is renewed. The turnover is not sudden. Cretan pygmy mammoth and the dwart hippopotamus disappeared, and Cretan deer and dwarf elephant arrived (3)														
Mus Zone FC Oceanic-like island of type 2 or island separated by a narrow sea (1). Low endemism, poor diversification (but more diversified thant previous FC), unbalanced. They probably arrived with "pendel route". Sites: Stavros Micro, Charoumbes 2, Charoumbes 3, among others	Middle to Late Pleistocene. Subdivided in two biozones: *M. bateae* and *M. minotaurus*	R	Muridae	*Mus bateae*	*M. musculus* (2)							?		Literature: 1, 2, 3, 4, 5. Single lineage. Progressive BS increment of *M. minotaurus*
		R	Muridae	*Mus minotaurus*								?		
		R	Muridae	*Kritimys catreus*	Previous FC							?		Literature: 2, 3, 4. *M. bateae* bizone: in older sediments. Minimal overlap of biozones (3)
		I	Soricidae	*Crocidura zimermanni*	*C. kornfeldi* (3)		?							Literature: 2, 3, 4. In both biozones. It is present in the extant fauna of Creta
		A	Cervidae	*Candiacervus ropalophorus*	The most likely candidates are: *C. peloponnesiacus* or a giant deer from the *Megaloceros verticornis* group (3)				MF					Literature: 2, 3, 4. This classification follows De Vos (9). Caloi and Palombo (10) named these species as: *Megaceroides* (*Candiacervus*) *ropalophorus*, *Megaceroides* (*Candiacervus*) *ropalophorus*, *Megaceroides* (*Candiacervus*) *cretensis*, ?*Pseudodama rethymnensis*, ?*Pseudodama* (*Leptocervus*) *dorothensis* and ?*Pseudodama* (*Leptocervus*) *major*
		A	Cervidae	*Candiacervus* sp. IIa					MF					
		A	Cervidae	*Candiacervus* sp. IIb					MF					
		A	Cervidae	*Candiacervus* sp. IIc					MF					
		A	Cervidae	*Candiacervus cretensis*					MF					

		A	Cervidae	*Candiacervus rethymnensis*					MF					respectively. *M. minotaurus* biozone. Endemic species. The two first species are the smallest and occupies a niche close to that of the wild goat. *C. rethymensis* is of medium BS. *C. major* is the gigantic morphotype. Sympatric speciation followed by an adaptive ratiation to occupy all posible empty niches ranging from dense forest to jagged rocks (11).
		A	Cervidae	*Candiacervus* sp. V or *C. dorothensis*					MF					
		A	Cervidae	*Candiacervus* sp. VI or *C. major*					MF					
		PR	Elephantidae	*Palaeoloxodon creutzburgi*	*P. antiquus*				MF					Literature: 1, 3, 4, 5. *M. minotaurus* biozone. Endemic. Little smaller. BM=2500kg
		PR	Elephantidae	*Palaeoloxodon antiquus*	*P. antiquus*				MF					Literature: 2, 3, 4. = *Palaeoloxodon chaniensis* (12). *M. minotaurus* biozone. Normal BS
		C	Mustelidae	*Lutrogale cretensis*	*L. perspicillata*	X	X							Literature: 3, 4, 13, 14. = *Isolalutra cretensis* (15). *M. minotaurus* biozone (Late Pleistocene). BM=11kg. Less aquatic. Its diet consisted mainly of fishes, with crustaceans and possibly small land vertebrates such as mice

The Mus Zone FC was extincted just before or after the arrival of the first humans on the island. The new fauna arrived with humans: *Martes foina bunites*, *Meles meles arcalus*, *Crocidura suaveolens caneae*, *Suncus etruscus*, among others (3). In Palombo et al. (4), *Hippopotamus* sp. are described in the *M. bateae* biozone; and *M. foina* and *M. meles* are described in the *M. minotaurus* biozone. Chiroptera order is observed in several localities (2)

The pre-Pleistocene mammalian fossils from Crete are continental taxa of a Late Miocene age. During Late Miocene and Early Pliocene it became fragmented into small pieces. It was largely submerged towards the end of Pliocene. Later (Pleistocene), it emerged again and has the present configuration (3). Bibliographic legend: (1) Marra 2005, (2) Alcover et al. 1981, (3) Van der Geer et al. 2010, (4) Palombo (2007), (5) Palombo (2009a), (6) Sondaar and Van der Geer (2005), (7) Palombo 2004, (8) Poulakakis et al. 2006, (9) De Vos 1979, (10) Caloi and Palombo 1996, (11) De Vos and Van der Geer 2002, (12) Symeonidis et al. 2000, (13) Masseti 2009, (14) Lyras et al. 2010, and (15) Willemsen 1992.

2. CYPRUS

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
Cyprus FC Oceanic-like island of type 2 (1,2). A unique FC is observed in Cyprus (stasis in an endemic island fauna). It is highly endemic, with an extremy low biodiversity, impoverished, and unbalanced. The dispersal moment can be at Middle Pleistocene (hippo and elephant) following a sweepstake route (1). Sites: Agios Phanentis, Aetokremnos Akrotiri, Asproyi, Vokolosspilios, Agia Napa, among others	Middle Pleistocene to Late Pleistocene-Holocene	R	Muridae	*Mus* sp.	?							?		Literature: 1, 2, 3. = *Mus cypriacus* (4,5), the extant form of *Mus* on the island
		I	Soricidae	*Crocidura suaveolens praecypria*	?		?							Literature: 1, 2, 3. Possible intrusion from Holocene deposits
		Q		*Rousettus aegyptiacus*	?					X				Literature: 1, 2, 3, 6. Late Pleistocene-Holocene. Fruit bats: 1-2 species
		A	Hippopotamidae	*Phanourios minor*	*Hippopotamus amphibus* (2)				B/G					Literature: 1, 2, 3, 6. = *Phanourios minutes* (7, 8). Present in all the Pleistocene. Endemic, abundant. Greatly reduced in BS (dwarf). It is adapted to terrestrial lifestyle (not running) (2). It shows similarities with *Hippopotamus amphibious*
		PR	Elephantidae	*Palaeoloxodon cypriotes*	*P. antiquus* (1,2)				MF					Literature: 1, 2, 3, 6, 7. Present in all the Pleistocene. Endemic, rare. It is remarkably reduced in BS (dwarf). BM=250kg
		C	Viverridae	*Genetta plesictoides*	*G. genetta*	X								Literature: 1, 2, 3, 9. Late Pleistocene-Holocene. Rare, larger than common genet. Possible intrusion from Holocene deposits

The faunal stasis was dramatically interrupted in the early Holocene, which led to the extinction of all Pleistocene fauna. Holocene of Cyprus is characterized by mainland fauna. Although rather impoverished, unbalanced and endemic at subspecies level (*Vulpes vulpes indutus*, *Ovis orientalis ohion*, *Rattus rattus*, *Rattus norvergicus*, *Mus musculus*, *C. suaveolens cypria* and 15 bat species) (2)

It is an island never connected to the mainland, and its origin was consequence of the volcanism activity. The extrem impoverishment of the island was the result of their oceanic origin and the large distance to the nearest mainland (2). Bibliographic legend: (1) Marra 2005, (2) Van der Geer et al. 2010, (3) Masseti 2009, (4) Bonhomme et al. 2004, (5) Gippoliti and Amori 2006, (6) Alcover et al. 1981, and (7) Sondaar and Van der Geer 2005, (8) Boekschoten and Sondaar 1972, and (9) Lyras et al. 2010.

3. GARGANO

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
Terra Rossa FC Gargano area was part of an archipelago during the Late Miocene and Early Pliocene (other islands: Le Murge). Rich endemic fauna, impoverished, and highly unbalanced. Arrival by filter corridor (1) or sweepstake dispersal (2, 3, 4). Polyphasic origin (3), possibly it was an impoverished relic of an older fauna (5). Bulk of endemic micromammals (rodents, lagomorphs and insectivores) and birds (some of which with gigantic BS). Macromammals are poorly represented. It was produced an in situ speciation. Fissures: Biancone 1, Rinascita 1, Trefossi 1, Cantatore 3A, Fina D, San Nazario 4, Fina H, Gervasio 1, Chiro 4, Gervasio 2, San Giovannino, F15, F21b, F21c, F1, F8, F9, F32	Late Miocene (6,7)	R	Muridae	*Apodemus* sp.	?							?		Literature: 6, 8. In some cases assigned to *A. gorafensis* (7). All fissures. Not endemic, common
		R	Muridae	Murinae nov. gen. et sp.	?			?						Literature: 9. Fissure M013. Possible ancestor of *Mikrotia*
		R	Muridae	*Mikrotia magna* (L4)	*Stephanomys* (10) or *Apodemus* (11)			X						Literature: 1, 6, 7, 8. Endemic, widespread. Represented by at least four lineages (differences in BS). *M. parva* from oldest fissures, *M. maiuscola* is the resident evolutionary lineage, and *M. magna* the very large-sized species (from another island) which is restricted to youngest fissures. Important BS increase and teeth changes (abrasive diet)
		R	Muridae	*Mikrotia parva* (L2)				X						
		R	Muridae	*Mikrotia maiuscola*				X						
		R	Muridae	*Mikrotia* L1				X						
		R	Muridae	*Mikrotia* L3				X						
		R	Gliridae	*Stertomys daamsi*	(?) *Myomimus* (12) or ancestor of the *Peridyromys-Myomimus* lineage (13)							?		Literature: 6, 7, 14. Intermediate endemic, common, small-sized group. Evolutionary trend in *S. daamsi-S. degiulii*, with a reduction in BS. Adaptive radiation
		R	Gliridae	*Stertomys simplex*								?		
		R	Gliridae	*Stertomys degiulii*								?		
		R	Gliridae	*Stertomys daunicus*	(?) *Myomimus* (12) or ancestor of the *Peridyromys-Myomimus* lineage (13)							?		Literature: 6, 7, 14. Intermediate endemic, rare, large BS. *S. laticrestatus* is the largest species. Possibly this species came from another neighbourhing island (Phase 2). Adaptive radiation
		R	Gliridae	*Stertomys lyrifer*								?		
		R	Gliridae	*Stertomys laticrestatus*								?		
		R	Gliridae	*Dryomys apulus*	(?) *Dryomis nitedula* (7)							?		Literature: 6, 7, 14. = *Eliomys* (15). Older fissures. Not endemic, rare
		R	Cricetidae	Cricetodontinae nov. gen. et sp.	?							?		Literature: 9 Fissure M013. Endemic
		R	Cricetidae	*Hattomys beetsi*	*Cricetulodon* (14) or *Apocricetus* (2)							?		Literature: 6, 7, 14. Intermediate endemic, common. They belong to a single phyletic lineage that increases in BS. They disappeared in the middle phase (7)
		R	Cricetidae	*Hattomys nazarii*								?		
		R	Cricetidae	*Hattomys gargantua*								?		

	Cricetidae	*Neocricetodon* sp.	?							?		Literature: 6, 7. = *Cricetulodon* (16). Older fissures. Not endemic
R	Cricetidae	*Apocricetus* sp.	*Rotundomys* or *Kowalskia*							?		Literature: 6, 7. = *Cricetus* (16). Older fissures. Not endemic
I	Erinaceidae	*Deinogalerix freudenthali*	*Parasorex* (4)	X						X		Literature: 6, 7, 8, 14. Strongly endemic. Relic of an older phase. Present in the most ancient fissures. It is the smallest species and the only. Precursor of 2 evolutionary lineages: *D. minor* and *D. intermedius*
I	Erinaceidae	*Deinogalerix minor*		X						X		Literature: 6, 7, 8. Strongly endemic. *D. freudenthali* > *D. minor* > *D. brevirostris*
I	Erinaceidae	*Deinogalerix brevirostris*		X						X		
I	Erinaceidae	*Deinogalerix intermedius*		X						X		Literature: 6, 7, 8. Strongly endemic. *D. freudenthali* > *D. intermedius* > *D. koenigswaldi*. The latter is the giant galericine insectivore of Gargano, observed only in the youngest fissures (BM=5-9kg). They ate small vertebrates, crustaceans and crabs
I	Erinaceidae	*Deinogalerix koenigswaldi*		X						X		
I	Erinaceidae	*Apulogalerix pusillus* (17)	*Parasorex* (4)		X							Literature: 1, 6, 7, 8, 14. = *Galerix* or *Parasorex* (6). All localities. Intermediate endemic, single lineage
I	Soricidae	*Lartetium* cf. *dehmi*	*Lartetium dehmi*		?					?		Literature: 6, 7, 14. Older fissures. Not endemic. Single lineage
L	Ochotonidae	*Prolagus imperalis*	*P. oeningensis* (18) or *P. oeningensis*-like *ancestor* (19)			X						Literature: 6, 7, 14. Intermediate endemic, widespread. Two lineages: the largest sized (*P. imperialis*) occurred in the youngest fissures (newcomer), the smallest (*P. apricenicus*) in all the fissure fillings. Important BS increase. Dominant element of youngest faunas. *P. imperialis* arrived likely due to dispersals from neighbouring islands of the archipelago
L	Ochotonidae	*Prolagus apricenicus*				X						
Q		Chiroptera	?									
A	Holiptomericidae	*Hoplitomeryx matthei*	*Micromeryx* (20), *Amphimoschus* (21), Palaeomerycidae (22), Paleogene “pre Pecora”			?						Literature: 6, 7, 14. Following the descriptions of Mazza and Rustioni (24). Several lineages evolved from the ancestral stock of colonizers
A	Holiptomericidae	*Hoplitomeryx apruthiensis*				?						

		A	Holiptomericidae	*Hoplitomeryx apulicus*	ruminant stock (14) or small-sized Tragulina representatives of western Asian (23)			?						giving rise to different species, similar morphologically to one another, but quite different in BS and proportions (24). It was a strongly endemic genus, relic of an older phase. The genus possesses five cranial appendages and sabre-like, moschid type upper canines. *H. falcidens* was small-sized. *H. magnus* was the largest, and *H. matthei* was the second largest representatives of the hoplitomerycids
		A	Holiptomericidae	*Hoplitomeryx falcidens*				?						
		A	Holiptomericidae	*Hoplitomeryx magnus*				?						
		A	Holiptomericidae	*Hoplitomeryx minutus*				?						
		C	Mustelidae	*Paralutra garganensis*	*P. jaegeri*							X		Literature: 6, 7, 14, 25. Slightly endemic, rare. Some skills for terrestrial lifestyle. Shellfish diet
Mainland FC	Early Pleistocene	In the last phase of Terre Rosse deposits, it is observed a critical drop in faunal diversity, which also affected the highly endemic small mammals. It may have been triggered by external geodynamic forces which shrank the Early Pliocene Gargano island short before its definitie disruption (14). The Pliocene flooding of the area led to the extinction of this peculiar fauna (7). The area emerged again and became firmly connected to the mainland in the Ealy Pleistocene (euroasiatic species): *Pachycrocuta brevirostris*, *Homotherium latidens*, *Megantereon megantereon*, *Acinonyx pardinensis*, *Canis mosbachensis*, *Equus altidens*, *Bison degiulii*, *Theropithecus* sp., *Allophaiomys ruffoi*, *Episoriculus gibberodon*, *Hystrix refossa*, among others (7)											

The different sites of Gargano (Terre Rosse deposits) have been ordered biochronologically, as a result of the evolution of murids, cricetids and ochotonids. Not all the species appear in all the fissures assessed. See Masini et al. (Table 4) for further details (6). Bibliographic legend: (1) Freudenthal 1971, (2) Freudenthal and Martín-Suárez 2010, (3) Masini et al. 2002, (4) van den Hoek Ostende 2001, (5) Butler 1980, (6) Masini et al. 2010, (7) Van der Geer et al. 2010, (8) Alcover et al. 1981, (9) Masini et al. 2013, (10) Freudenthal 1976, (11) Freudenthal and Martín-Suárez 1999, (12) Freudenthal and Martín-Suárez 2006, (13) Rinaldi 2006, (14) Masini et al. 2008, (15) De Giuli et al. 1987, (16) Freudenthal 1985, (17) Masini and Fanfani 2013, (18) Mazza et al. 1995, (19) Angelone 2007, (20) Moyà-Solà et al. 1999, (21) Leinders 1984, (22) Van der Geer 2008, (23) Mazza 2013, (24) Mazza and Rustioni 2011, and (25) Lyras et al. 2010.

4. GYMNESIC ISLANDS (MALLORCA, MENORCA AND NEARLY 30 SURROUNDING ISLETS)

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
MALLORCA														
Myotragus palomboi FC	Early Pliocene 5.3 Mya	A	Bovidae	*Myotragus palomboi*	?				B					Literature: 1
New faunal complex that entered to the islands during the Messinian Salinity Crisis (5.35 Mya). Site: Caló d'en Rafelino		L	Leporidae	*Hypolagus balearicus*	?			?						Literature: 2
		R	Gliridae	cf. *Hypnomys*	*Eliomys truci*							?		Literature: 3
		R	Cricetiae	*Tragomys macpheei*	*Apocricetus*							?		Literature: 3 Large
		I	Soricidae	*Nesiotites rafelinensis*	*Episoriculus*		?							Literature: 4, but see against opinions at 5
Myotragus pepgonellae FC	Early Pliocene	A	Bovidae	*Myotragus pepgonellae*	Previous FC				B					Literature: 6, 7. = *Insulotragus pepgonellae* (8) = *Myotragus pepgonellai* (9, but see 10) BM=60kg
Impoverished and unbalanced. Sites: Cala Morlanda, sa Penya Roja, among others		R	Gliridae	cf. *Hypnomys*	*Eliomys truci*							?		Literature: 6. It is not assigned to any particular species
		I	Soricidae	cf. *Nesiotites*	*Episoriculus* (11)		?							Literature: 6
Myotragus antiquus FC	Middle Pliocene	A	Bovidae	*Myotragus antiquus*	Previous FC				B					Literature: 6, 7. = *Insulotragus antiquus* (8)
		R	Gliridae	*Hypnomys waldreni*	Previous FC							?		Literature: 6, 7, 12
		I	Soricidae	*Nesiotites ponsi*	Previous FC		?							Literature: 6, 12. = *Asoriculus*, *Episoriculus*, *Soriculus ponsi*
Myotragus kopperi FC	Plio-Pleistocene boundary	A	Bovidae	*Myotragus kopperi*	Previous FC				B					Literature: 6. Endemic
Oceanic-like island of type 1 (13). High endemic, unbalanced fauna. Evolution *in situ*: no extinctions and no arrivals. Sites: Sa Pedrera de S'Ònix, among others		R	Gliridae	*Hypnomys onicensis*	Previous FC							?		Literature: 6, 12. = *H. intermedius* (14) = *Eliomys onicensis*
		I	Soricidae	*Nesiotites* aff. *ponsi*	Previous FC		?							Literature: 6. = *Asoriculus*, *Episoriculus* or *Soriculus* aff. *ponsi*. Site: Sa Pedrera de S'Ònix

Myotragus and associated fauna appear in all of the Menorcan Pleistocene and Holocene deposits. Probably, this is consequence of the glaciations and the related melting of both islands (15). The Mallorcan fauna invaded Menorca in the Late Pliocene or Early-Middle Pleistocene (12)

***Myotragus batei* FC**	Early-Middle Pleistocene	A	Bovidae	*Myotragus batei*	Previous FC				B					Literature: 6, 7. = Synonymized to *M. binigausensis* and renamed and emended as *M. bateae* (9, but see 10,16,17). Endemic
Oceanic-like island of type 1 (13). High endemism, unbalanced fauna. Evolution *in situ*: no extinctions and no arrivals		R	Gliridae	*Hypnomys onicensis*	Previous FC							?		Literature: 6. = *H. intermedius* (14) or *Eliomys onicensis*. Endemic
		I	Soricidae	*Nesiotites hidalgo*	Previous FC		?							Literature: 6. = *N. hidalgoi* (8) = *Soriculus*, *Asoriculus* or *Episoriculus hidalgo*(*i*) (18)
***Myotragus balearicus* FC**	Late Pleistocene to Holocene of Mallorca and Menorca	A	Bovidae	*Myotragus balearicus*	Previous FC				B					Literature: 6, 7. Endemic. BM=23kg
Oceanic-like island of type 1 (13). Very high endemism, unbalanced fauna. Evolution *in situ*: no extinctions and no arrivals		R	Gliridae	*Hypnomys morpheus*	Previous FC							?		Literature: 6, 12. = *H. mahonensis* (19) or *Eliomys morpheus* (8). Endemic
		I	Soricidae	*Nesiotites hidalgo*	Previous FC		?							Literature: 6, 12. = *N. hidalgoi* (8) or *Soriculus*, *Asoriculus* or *Episoriculus hidalgo*(*i*) (18)
The extinction of the endemic fauna of Gymnesic Islands is related to the arrival of humans (8)														

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
MENORCA														
***Nuralagus rex* FC**	Early/Middle Pliocene	I	Leporidae	*Nuralagus rex*	?									Literature: 6, 7. Endemic. Giant
This FC is not recorded in Pleistocene deposits, suggesting that it disappeared from this island before then		R	Gliridae	*Murscardinus cyclopeus*	?							?		Literature: 6, 7. Endemic. Giant
		Q	Rhinolophidae	*Rhinolophus* cf. *grivensis*	?		?							Literature: 6
Myotragus and associated fauna appear in all of the Menorcan Pleistocene and Holocene deposits. Probably, this is consequence of the glaciations and the related melting of both islands (15). The Mallorcan fauna invaded Menorca in the Late Pliocene or Early-Middle Pleistocene (12)														
***Myotragus batei* FC**	Early Pleistocene (20)	A	Bovidae	*Myotragus binigausensis*	?				B					Literature: 6, 7. = Synonymized to *M. batei* and renamed and emended as *M. bateae* (9, but see 10,16,17)
Oceanic-like island of type 1 (13). High endemism, unbalanced fauna. Evolution *in situ*: no extinctions and no arrivals		R	Gliridae	*Hypnomys eliomyoides*	?							?		Literature: 6. = *H. onicensis* (21)
		I	Soricidae	*Nesiotites meloussae*	?		?							Literature: 6. = *N.* aff. *ponsi* (21)

***Myotragus balearicus* FC**	Late Pleistocene to Holocene	A	Bovidae	*Myotragus balearicus*	Previous FC				B					Literature: 6, 7. Endemic. BM=23kg
Oceanic-like island of type 1 (13). Very high endemism, unbalanced fauna. Evolution *in situ*: no extinctions and no arrivals		R	Gliridae	*Hypnomys morpheus*	Previous FC							?		Literature: 6, 12. = *H. mahonensis* (19) or *Eliomys morpheus* (8). Endemic
		I	Soricidae	*Nesiotites hidalgo*	Previous FC		?							Literature: 6, 12. = *N. hidalgoi* (8) or *Soriculus*, *Asoriculus* or *Episoriculus hidalgo*(i) (18)
The extinction of the endemic fauna of Gymnesic Islands is related to the arrival of humans (8)														

At the beginning, the two main islands (Mallorca and Menorca) had a different paleogeographical history. Later, they were connected and had peculiar faunal sucessions. Bibliographic legend of tables: (1) Bover et al. 2010, (2) Quintana et al. 2010, (3) Agustí et al. 2012, (4) Rofes et al. 2012 (5) Furió and Pons-Monjo (2013), (6) Bover et al. 2008, (7) Sondaar and Van der Geer (2005), (8) Bover and Alcover 2008, (9) Bover and Alcover 2000, (10) Quintana 2004, (11) Reumer 1984, (12) Van der Geer et al. 2010, (13) Marra 2005, (14) Reumer 1994, (15) Cuerda 1975, (16) Moyà-Solà et al. 2007, (17) Jordana et al. 2013, (18) Made 1999, (19) Bate 1918, (20) Pons-Moyà et al. 1981, and (21) Reumer 1982.

5. SARDINIA AND CORSICA

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
***Oreopithecus* - Fiume Santo FC**	Late Miocene (Tortonian to Early Messinian) MN12-13	R	Muridae	*Huerzelerimys turoliensis*	?							?		Literature: 1, 2, 3. *Huerzelerimys turoliensis* = *Valerymys turoliensis* (4). Other authors attributed this element to *H. vireti* (5). From the lowest layer of Baccinello (V0)
During Late Miocene, a "Tusco-Sardinian paleobioprovince" came into existence as an isolated region, possibly as an archipelago. Endemic, quite diversified, and unbalanced. Fiume Santo indicates that a major connection was established between Sardinia and Maritime Tuscany and also (indirectly) with the African continent (1). Pre-Messinian connections with Corsica related to sea-level changes. Sites: Fiume Santo, Monte Bamboli and Baccinello-Cinigiano basin of the Maremma		R	Muridae	*Huerzelerimys oreopitheci*										Literature: 1, 2, 3, 5. *Huerzelerimys oreopitheci* = *Valerymys oreopitheci* (4). Lower level of Baccinello (V1). This fauna is not present in Fiume Santo, with the exception of *H. oreopitheci*. Previously, *Kowalskia* sp. was assigned in this layer, but further studies did not identified it (5)
		R	Muridae	*Anthracomys majori*	?							?		
		R	Muridae	*Parapodemus* sp. II	?							?		
		R	Gliridae	Gliridae nov. gen. et sp.	?							?		
		R	Gliridae	*Anthracoglis marinoi*	?							?		
		L	Ochotonidae	*Paludotona Etruria*	?			?						
		I	Soricidae	cf. *Crocidosorex*	?		?							
		R	Muridae	*Anthracomys majori*	?							?		Literature: 3, 5. Upper level of Baccinello (V2). This fauna is not present in Fiume Santo, with the exception of *A. lorenzi* which is also present in level V3
		R	Muridae	*Parapodemus* sp. I	?							?		
		R	Gliridae	*Anthracoglis lorenzi*	?							?		
		L	Ochotonidae	*Paludotona* aff. *etruria*	?			?						
		I	Soricidae	Indet.	?		?							
		R	Muridae	*Apodemus etruscus*	?							?		Literature: 5. From the Uppest level of Baccinello (V3). This fauna is not present in Fiume Santo. In this level, 3 species of Muridae indet. were also found
		R	Cricetidae	*Celadensia grossetana*	?							?		
		R	Cricetidae	*Kowalskia nestori*	?							?		
		R	Gliridae	*Muscardinus* aff. *vireti*	?							?		
		R	Gliridae	*Anthracoglis engesseri*	?							?		Literature: 5. From Fiume Santo. One molar found in V2 level of Baccinello
		R	Gliridae	*Anthracoglis* nov. sp.	?							?		Literature: 5. From Fiume Santo
		A	Suidae	*Eumaiochoerus* cf. *etruscus*	?							X		Literature: 1, 2, 3. = *Hippopotamodon*/*Microstonyx*. In Fiume Santo and V2 layers from Baccinello. Endemic traits

		A	Giraffidae	*Umbrotherium azzarolii*	*Sardomeryx* (3)			?						Literature: 1, 2, 3. In Fiume Santo and V2 layer from Baccinello. Endemic traits. Two Giraffidae: small and medium BS
		A	Bovidae	*Tyrrhenotragus* cf. *gracillimus*	?			?						Literature: 2. Other authors: *Tyrrhenotragus gracillimus* (1,3). In Fiume Santo and V1 (*T.* aff. *gracillimus*) and V2 layers (*T. gracillimus*) from Baccinello. Endemic traits
		A	Bovidae	*Turritragus casteanensis*	?			?						Literature: 2, 3. In Fiume Santo and V1 layer from Baccinello. Endemic traits. Early ascribe to *Maremmia haupti* (4)
		A	Bovidae	*Maremmia* aff. *lorenzi*	?			?						Literature: 2. Other authors: *Maremmia* cf. *lorenzi* (3) or *Maremmia lorenzi* (1). In Fiume Santo and V2 layer (*M. lorenzi*) from Baccinello. Endemic traits. Slightly larger. The commonest taxon
		A	Bovidae	Neotragini indet.	?			?						Literature: 1, 2, 3. In Fiume Santo and V1 and V2 layers from Baccinello. Endemic traits
		A	Bovidae	*Etruria viallii*	?			?						Literature: 1, 2, 3. In Fiume Santo and V1 layer from Baccinello. Endemic traits
		C	Ursidae	*Agriotherium anthracite*	?							X		Literature: 1, 3. = *Indarctos anthracitis* (2). Occurrence uncertain
		PI	Hominidae	*Oreopithecus bambolii*	?				X					Literature: 2, 3. Other authors: *Oreopithecus* cf. *bambolii* (1). In Fiume Santo and V1 and V2 layers (*O. bambolii*) from Baccinello. Endemic, highly derived
		C	Mustelidae	*Mustela major*	?	X								Literature: 3. In Fiume Santo
		C	Lutrinae	*Tyrrhenolutra helbingi*	?	X								Literature: 3. In V1 from Baccinello
		C	Lutrinae	*Paludolutra maremmana*	?	X						X		Literature: 3. In V2 from Baccinello
		C	Lutrinae	*Paludolutra campanii*	(?) *Tyrrhenolutra helbingi* (3)	X						X		Literature: 3. = *Lutra campanii* In V2 from Baccinello

NESOGORAL FC	Pliocene and the beginning of Pleistocene. Local evolution of some lineages, a reduced extinction rate and a moderate immigration rate													
Capo Mannu - Mandriola SubC	Middle to Late Pliocene (MN15) Early to Middle Pliocene	R	Muridae	*Rhagapodemus azzarolii*	*R. ballesioi* (3,6)							?		Literature: 1, 3, 7, 8, 9. Endemic ancestor of *Rhagamys*. Smaller
Continental island. Impoverished and balanced. Colonization using a land bridge (sea drop) from Europe. Artiodactyls could have reached the island during the Late Miocene, and small mammals could have entered later. All the fauna was practically renewed with the exception of *Tyrrhenoglis* sp. Sites: Su Casteddu, Campidanu, Mandriola, Orosei, among others		R	Muridae	*Apodemus mannu*	?							?		Literature: 1, 3, 7, 8, 9, 10. Large. Restricted to this phase
		R	Gliridae	*Tyrrhenoglis* aff. *figariensis*	?							?		Literature: 1, 3, 7, 8. = *Eliomys* aff. *figariensis* Belonging to Miocene FC. Smaller than *T. majori*
		I	Erinaceidae	*Parasorex depereti*	*P. depereti*									Literature: 11
		I	Erinaceidae	Indet.	?		?							Literature: 1, 7, 9. Restricted to this phase
		I	Soricidae	*Asoriculus gibberodon*	*A. gibberodon*									Literature: 11. Possible ancestor of *Nesiotites*
		I	Soricidae	cf. Soricini indet.	?									Literature: 11
		I	Talpidae	*Talpa* cf. *minor*	*T. minor*									Literature: 11. Other authors: *Talpa* sp. (1,3,7,8). Possible ancestor of *T. tyrrhenica*
		L	Ochotonidae	*Prolagus* aff. *figaro*	*P. sorbinii* (12)			?						Literature: 12. Other authors: *Prolagus figari* (10), *Prolagus* sp. (1) or *Prolagus* aff. *sorbinii* (3). Small BS. Ancestor of *P. figaro* and *P. sardus*
		L	Leporidae	Gen. et sp. indet.	?			?						Literature: 12. Capo Mannu D1 (12)
		Q	Vespertilionidae	Bats	?									Literature: 7, 9
		A	Suidae	*Sus* aff. *sondaari*	*S. arvernensis* (3)							X		Literature: 1, 8. Other authors: *Sus sondarii* (3,7,10). BS decrease. Smaller than Capo figari one
		A	Bovidae	*Nesogoral* sp.	*Gallogoral*				MF					Literature: 1, 8
		C	Hyaenidae	*Chasmoporthetes*	?	X							?	Literature: 1, 8, 10. Its presence is supposed as a result of the cursorial skills of the herbivores
		In this FC, some authors (1,8) also described *Tyrrhenoglis* aff. *majori* (Rodentia. Gliridae)												
Capo Figari I/Orsei I SubC	Late Pliocene to Early Pleistocene	R	Muridae	*Rhagapodemus minor*	Previous FC							?		Literature: 1, 3, 7, 8, 9. = *Rhagamys minor* (6,13). Small
Oceanic-like island of type 1 (7). Low endemism, impoverished and ecologically balanced.		R	Gliridae	*Tyrrhenoglis* cf. *majori*	Previous FC							?		Literature: 1. Other authors: *Tyrrhenoglis* sp. (7). In some literature is also desribed in this FC *T. figariensis* (7)
		I	Talpidae	*Talpa* sp.	Previous FC		?							Literature: 1, 3, 7

The newcomers could arrive by sweepstake route during the Late Pliocene. Important dispersal of large-sized mammalian taxa. The profusion of goat-like bovids is indicative of a vicariance effect in a predator-poor environment. Sites: Orosei, Campo Figari, Capu Mannu, Monte Tuttavista, among others		I	Soricidae	*Nesiotites* sp. 2	?		?							Literature: 7, 13. Other authors: *Asoriculus* aff. *gibberodon* (3) or *Asoriculus* sp. (1). = *Asoriculus*, *Episoriculus* or *Soriculus*
		L	Ochotonidae	*Prolagus figaro*	Previous FC			?						Literature: 1, 7, 9
		L	Leporidae	*Oryctolagus* aff. *lacosti*	Previous FC			?						Literature: 1, 2. Species and genus doubtful (3)
		A	Suidae	*Sus sondaari*	Previous FC							X		Literature: 1, 3, 7, 8. Endemic of small BS. More cursorial
		A	Caprinae	Caprinae indet.	?			?						Literature: 3, 7
		A	Bovidae	*Nesogoral melonii*	Previous FC				MF					Literature: 1, 3, 8. = *"Antilope" melonii* (9)
		A	Bovidae	*Nesogoral* sp. > *N. cenisae*	Previous FC				MF					Literature: 1, 3, 8.
		A	Bovidae	*Asoletragus gentry*	?				MF					Literature: 1, 3. Small BS
		A	Cervidae	Dwarf cervid	?			?						Literature: 9
		C	Mustelidae	*Mustela putorius*	?	?								Literature: 1. Other authors: *Mustela* sp. (8)
		C	Mustelidae	*Pannonictis* sp.	*P. nestii*	?								Literature: 1, 3, 8, 14
		C	Mustelidae	*Enhydrictis galictoides*	*Pannonictis nestii*	?								Literature: 9, 14
		C	Hyaenidae	*Chasmaporthetes melei*	*Chasmaporthetes lunensis*	X							?	Literature: 1, 3, 8. Similar to *C. lunensis*, but slightly smaller size. Prey on *Nesogoral*
		PI	Chercopithecidae	*Macaca* aff. *majori*	*M. florentina* (3)			?						Literature: 8. Other authors: *Macaca majori* (3,9). Smaller
MICROTUS FC	The transition between biozones is not sharp, because remains of newcomers and previous endemic species were found together													
Orosei 2 SubC	Late Early Pleistocene to Middle Pleistocene	R	Muridae	*Rhagapodemus minor*	Previous FC							?		Literature: 1, 3, 7, 8, 15. = *Rhagamys minor* (6,13)
		R	Gliridae	*Tyrrhenoglis majori*	Previous FC			X						Literature: 8
		R	Cricetidae	*Microtus* (*Tyrrhenicola*) *sondaari* > *henseli*	*M.* (*Allophaiomys*) *ruffoi* (3)							?		Literature: 1, 3, 7. Other authors: *Microtus* n. sp. (8,15). = *Pitimys henseli*
		I	Talpidae	*Talpa tyrrhenica*	Previous FC		?							Literature: 1, 3, 15
		I	Soricidae	*Nesiotites* sp. 1	Previous FC		?							Literature: 7, 13. Other authors: *Asoriculus similis* (1,3,15). Medium BS with terrestrial habits. In Corsica *Asoriculus corsicanus*

		L	Leporidae	*Oryctolagus* aff. *lacosti*	Previous FC			?						Literature: 1, 8, 15
		L	Ochotonidae	*Prolagus figaro*	Previous FC			?						Literature: 1
		A	Bovidae	Caprinae indet.	Previous FC			?						Literature: 7, 8, 15
		A	Cervidae	*Megaloceros* or *"Praemegaceros"* sp. > *Megaloceros* or *"Praemegaceros" sardus*	Megacerines of the verticornis group (*M. verticornis* or *M. solilhacus*) or forms close to *Eucladoceros tetraceros* (3)				MF					Literature: 1, 3, 8, 15. In Corsica it is described with *Megaloceros* an endemic red deer (*Cervus elaphus rossii*) during the Middle Pleistocene, which is smaller in BS
		C	Mustelidae	*Enhydrictis* sp.	Previous FC	?								Literature: 1 Occurence uncertain
		C	Mustelidae	*Pannonictis* sp.	Previous FC	?								Literature: 1, 7. Other authors: *Pannonictis nestii* (15)
		C	Canidae	*Cynotherium* sp.	*Xenocyon* (3)	?								Literature: 1, 3, 7, 8, 15
		PI	Chercopithecidae	*Macaca majori*			?							Literature: 1, 7, 15. Occurrence uncertain in the next FC
		In this FC, some authors (15) also described *Tyrrhenoglis figarensis* (Rodentia, Gliridae)												
Dragonara SubC	Late Middle Pleistocene to Early Holocene	R	Muridae	*Rhagamys orthodon*	Previous FC							?		Literature: 1, 3, 8, 9, 10, 15. Large BS and hypsodonty
		R	Cricetidae	*Microtus* (*Tyrrhenicola*) *henseli*	Previous FC							?		Literature: 3, 7, 8, 10, 15
		R	Gerbillidae	Gerbillidae gen. et sp. indet.										Literature: C. Angelone (personal comment)
		I	Talpidae	*Talpa tyrrhenica*	Previous FC		?							Literature: 1, 7, 8, 9
		I	Soricidae	*Nesiotites* sp. 1	Previous FC		?							Literature: 7, 13. Other authors: *Asoriculus similis* (1,7,8,15)
		L	Ochotonidae	*Prolagus sardus*	Previous FC			?						Literature: 1, 7, 8, 9, 10, 15
		A	Cervidae	*Megaloceros* or *"Praemegaceros" cazioti*	Previous FC				G	X				Literature: 1, 3, 7, 8, 10, 15. Decrease in BS from previous FC. BM=70 kg
		PR	Elephantidae	*Mammuthus lamarmorai*	*M. trogontherii*				?B/ MF					Literature: 1, 3, 7, 8, 10, 15. = *M. lamarmorae*. Smaller. BM=800kg
		C	Mustelidae	*Enhydrictis galictoides*	Previous FC	X								Literature: 1, 3, 15. Occurence uncertain
		C	Mustelidae	*Algarolutra majori*	*L. simplicidens*	X								Literature: 1, 3, 8, 14, 15. = *Cyrnaonyx* (8) Late Pleistocene

		C	Mustelidae	*Sardolutra ichnusae*	*L. simplicidens* or *Cyrnolutra castiglionis*	X								Literature: 1, 3, 8, 14, 15. = *Nesolutra* (16) Late Pleistocene/Holocene. Small BS and acquatic life (marine)
		C	Mustelidae	*Megalenhydris barbaricina*	*L. simplicidens*	X								Literature: 1, 3, 8, 14, 15. Late Pleistocene/Holocene
		C	Canidae	*Cynotherium sardoum*	Previous FC	X								Literature: 1, 3, 7, 8, 10, 15. Smaller endemic predator. BM=12kg. Probably prey on *P. sardus* and calves of "*P.*" *cazoti*
		In this FC, some authors (3) also described *Cyrnolutra castiglionis* (=*Lutra*) (Carnivora, Mustelidae) from the Middle Pleistocene. It had a small BS and an acquatic life. Its probable ancestor was *Lutra simplicidens*												
The large mammals of the last FC disappeared first followed by small mammals (17). Last species included only small mammals (e.g. *Tyrrhenicola*, *Prolagus* and *Asoriculus*)														

Sardinia and Corsica have a shared history until the start of the Holocene. The post-Miocene taxa of Sardinia and Corsica were slightly endemic as a result of the large island area and the proximity to the mainland. During Early to Late Miocene, Sardinia and Corsica formed a unit with lands that today are part of Tuscany on the Tyrrhenian site. It might be that the region consisted of several large islands, forming an archipelago, as is indicated by small differences between the mutual faunas (3). Later, Tuscany became connected to the continent and Sardinia and Corsica became isolated again. Bibliographic legend: (1) Masini et al. 2008, (2) Palombo 2009b, (3) Van der Geer et al. 2010, (4) Mein et al. 1993, (5) Casanovas-Vilar et al. 2011, (6) Angelone and Kotsakis 2001, (7) Marra 2005, (8) Palombo 2006, (9) Alcover et al. 1981, (10) Sondaar and Van der Geer 2005, (11) Furió and Angelone 2010, (12) Angelone et al. 2015, (13) Abbazzi et al. 2004, (14) Lyras et al. 2010, (15) Palombo (2007), (16) Willemsen 1992, and (17) Palombo et al. 2004.

6. SICILY

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
Monte Pellegrino FC	Late Pliocene-Early Pleistocene	R	Muridae	*Apodemus maximus*	?							?		Literature: 1, 3, 4, 5, 6, 7, 8, 9. Endemic. Relic on an older fauna. It is twice as large as the living *A. sylvaticus* (large BS)
Sicily was made up of two islands (archipelago, oceanic-like island of type 2) (1,2). Very high endemisms (of micrommmals), poorly diversified, impoverished and unbalanced fauna. They probably used the archipelago route. Polyphasic origin: North African and European forms.Its composition suggests that it may have derived in part from an older population phase (2). Malta was emergent. Site: Monte Pellegrino (karst cavity)		R	Gliridae	*Leithia* sp.	*Eliomys* sp. (2,10)							?		Literature: 1, 3, 4, 6, 8. Relic of an older fauna. Endemic. Possible precursor of *Leithia* and *Maltamys* from the Middle/Late Pleistocene of Sicily
		R	Gliridae	*Maltamys* cf. *gollcheri*	?							?		Literature: 1, 3, 6, 7, 8. Some authors: *Maltamys* sp. (2,9) or cf. *Maltamys* (5). Endemic. Relic of an older fauna. Large BS
		R	Ctenodactylidae	*Pellegrinia panormensis*	African Ctenodictilids (5)							?		Literature: 1, 3, 4, 5, 6, 7, 8, 9. Strongly endemic of large BS. North-African origin (11)
		I	Soricidae	*Asoriculus burgioi*	*Asoriculus* mainland		?							Literature: 1, 3, 6, 8, 9. = *Episoriculus* sp. (5,7). Endemic. Relic of an older fauna. Large BS. Uncertain origin (Europe or Africa)
		L	Leporidae	*Hypolagus peregrinus*	European form			?						Literature: 6, 9. Some authors: *Hypolagus* sp. (3,5,7,8). Moderate endemism. European origin. Less cursorial (12)
		C	Mustelidae	*Mustelercta arzilla*	*Pannonictis nestii*	?								Literature: 4, 5, 6, 7, 9, 13. = *Pannonictis arzilla* (1,3,8,14). Moderate endemism. European origin
All the mammals of Monte Pellegrino are apparently extinct in the next FC, excepting *Maltamys* cf. *gollcheri*. Volcanic activities or submering of the island occurred (5)														
Palaeoloxodon falconeri FC	early Middle Peistocene (0.7-0.3 Mya)	R	Gliridae	*Leithia cartei*	Previous FC							?		Literature: 1, 3, 5, 7, 8, 16. Endemic. Small and rare. From previous FC
Archipelago (two islands), ocenic-like island of type 2 (1, 5). Highly endemic, low		R	Gliridae	*Leithia melitensis*	Previous FC							?		Literature: 1, 3, 5, 6, 7, 8, 9, 16. Endemic. Of large BS. From previous FC

biodiversity, impoverished, unbalanced. Extinction of the small mammals for the previous FC excepting dormice. The entrance was by archipelago route, sweepstake dispersal or filter bridge. Strongly isolated from the mainland with difficult barrier. Polyphasic origin. Malta is emerged. This FC is typical of the Sicilian Siculo-Maltense archipelago (connection with Malta) (15). Sites: Spinagallo, Comiso, Chiaramonte Gulfi, Contrada Annunziata, among others		R	Gliridae	*Maltamys gollcheri*	Previous FC							?		Literature: 1, 3, 6, 8, 9. For several authors (16): *Maltamys* sp. ex gr. M. *gollcheri-wiedincitensis*. = *Eliomys gollcheri*. From previous FC Endemic.
		I	Soricidae	*Crocidura sicula esuae*	(?) *C. tarfayaensis* (17)		?							Literature: 1, 3, 6, 7, 8, 9. = *C. esuae* or *esui* (18). Endemic. Larger BS. Uncertain orgin, probably from North Africa
		Q		Several sp. of bats	Indet.									Literature: 6, 8
		PR	Elephantidae	*Palaeoloxodon falconeri*	*P. antiquus*				MF /B					Literature: 1, 3, 6, 7, 8, 9. Endemic. Strongly reduced in BS, dwarf (90 cm at shoulders). BM=100-170kg. It is also suggested a *Mammuthus* origin (19). Initially, it is described *P. melitensis* that is just the larger form of this sexually dimorphic species (20)
		C	Mustelidae	*Nesolutra trinacriae*	?	X								Literature: 1, 3, 8, 16. = *Lutra trinacriae* (6,7,9). Endemic. Slightly smaller
		C	Canidae	*Vulpes* sp.	*Vulpes* sp.	X								Literature: 1, 8, 9, 16. Occurrence uncertain
		C	Ursidae	*Ursus* sp.	*Ursus* sp.							X		Literature: 1, 8, 9, 16. Occurrence uncertain
The next FC is almost completely renewed with respect to the previous one (excepting micromammals). *P. falconeri* was extinct and the faunal composition is more balanced and includes top predators such as the lion and hyena. However, there is a general absence of perissodactyls														
***Palaeoloxodon mnaidriensis* FC**	Late Middle Pleistocene to Early Late Pleistocene (9) 0.3-0.02 Mya	R	Gliridae	*Leithia* cf. *melitensis*	Previous FC							?		Literature: 1, 3, 8, 16. For several authors (5, 6, 7, 9): *Leithia melitensis*. Endemic
Oceanic-like island of type 2 (1). Moderate endemic, quite diversity, impoverished and balanced from a trophic point of view (presence of carnivores). They arrived by sweepstake route, “steeping stone” dispersal, pendel route in *P. mnaidriensis* or overland. Several migratory waves or temporary connections with mainland. There is some type of fiter that prevented small mammals from reaching the		R	Gliridae	*Maltamys* cf. *wiedincitensis*	Previous FC							?		Literature: 1, 3, 8. For several authors: *Maltamys wiedincitensis* (6,7,9) or *Maltamys* sp. ex gr. *M. gollcheri-wiedincitensis* (16). = *Eliomys wiedincitensis*. Endemic
		I	Erinaceidae	*Erinaceus europaeus*	*E. europaeus*		?							Literature: 1, 3, 6, 8
		I	Soricidae	*Crocidura* aff. *sicula esuae*	Previous FC		?							Literature: 1, 3, 8, 16. Other authors: *Crocidura sicula esuae* (6,7,9). = *C.* (aff.) *esuae* or *esui* (18). Endemic
		A	Suidae	*Sus scrofa*	*S. scrofa*							X		Literature: 1, 3, 6, 7, 8, 9, 16. Continental taxa

islands. Thus, small mammals are the survivors of the ancient FC, while large mammals arrived from Italy. It is a larger island with diversified environments. Malta also contained some of these taxa during this period, but some species were absent (15). Malta had a more impoverished fauna during this period. Sties: Maccagnone, Spinagallo, Coste di Gigia, Acquedolci, Maddalena Peninsula, Contrada Cimillà, Puntali Cave, among others		A	Bovidae	*Bos primigenius siciliae*	*B. primigenius*				G					Literature: 1, 3, 5, 6, 7, 8, 9, 16. Endemic. Moderately modified. 20% smaller
		A	Bovidae	*Bison priscus sicliliae*	*B. priscus*				G					Literature: 1, 3, 5, 6, 7, 8, 9, 16. Endemic. Moderately modified. 20% smaller
		A	Cervidae	*Cervus elaphus siciliae*	*C. elaphus*				MF					Literature: 1, 3, 6, 7, 8, 9, 16. Endemic. Moderately modified. 20-25% smaller. It was not a real dwarf
		A	Cervidae	*Dama carburangelensis*	*D. dama* cf. *tiberina* (21)				MF					Literature: 1, 3, 6, 8, 9, 16. = *Megaceros, Megaceroides* or *Praemegaceros carburangelensis* (7,8,10,21). Endemic. Moderately modified. 20-25% smaller. It was not a real dwarf
		A	Hippopotamidae	*Hippopotamus pentlandi*	*H. amphibius*				G					Literature: 1, 3, 5, 6, 7, 8, 9, 16. Endemic. Moderately modified. 10-15% smaller. It is not a real dwarf
		PR	Elephantidae	*Palaeoloxodon mnaidriensis*	*P. antiquus*				MF /B					Literature: 1, 3, 5, 6, 7, 8, 9, 16. Endemic. BM=2500kg. Initially, it is described *P. antiquus leonardi* that is just the larger form of this sexually dimorphic species
		C	Mustelidae	*Nesolutra trinacriae*	*L. simplicidens*	X								Literature: 1, 3, 8. = *Lutra trinacriae* (6,9). Endemic
		C	Canidae	*Canis lupus*	*C. lupus*	X								Literature: 1, 3, 5, 6, 7, 8, 9, 16. Not endemic. Prey on cervids (2)
		C	Felidae	*Panthera leo spelaea*	*P. leo*	X								Literature: 5, 7, 9. For some authors: *Panthera leo* (1,6,8) or *Panthera spelaea* (3,16). Prey on cervids (2)
		C	Hyaenidae	*Crocuta crocuta* cf. *spelaea*	*C. crocuta*	X							X	Literature: 1, 3, 8. For some authors: *Crocuta crocuta spelaea* (7,9) or *Crocuta crocuta* (6,16). Not endemic. Prey on cervids (2)
		C	Ursidae	*Ursus* cf. *arctos*	*U. arctos*							X		Literature: 1, 3, 8, 16. For some authors: *Ursus arctos* (6,7,9). Not endemic
		In this FC, some authors (2,9,16) also described *Vulpes vulpes* (Carnivora, Canidae) and *Microtus* (*Terricola*) sp. (Rodentia, Cricetidae). The remains initially described as *Megaceros* (*Megaceroides*) *calabriae* was later attributed to *Dama dama* cf. *tiberina* (21)												

Equus hydruntinus FC	Late Pleistocene	All the ungulates were replaced by mainland taxa of normal BS (without endemic features). This event occured during the sea level fall most important since Miocene (eustatic low stand). The FC change is not abrupt (no extinction of *P. mnaidriensis*)												
Grotta San Teodoro, Contrada Pianetti FC	Early Last Glacial 32000± 4000 years Before Present	R	Muridae	*Apodemus* cf. *sylvaticus*	*A. sylvaticus*							?		Literature: 1, 3, 8, 9, 16. Some authors: *Apodemus sylvaticus* (6). Not endemic. In the extant fauna
Island separated by a narrow sea (1). Low endemism (only *C.* cf. *sicula*), low diversity and balanced. They arrived by pendel route or "steeping stone" dispersal, although it is also suggested a total connection with the mainland (land bridge) without any filter. There were the extinction of some species (hippos, endemic dormice and others) and the entrance of the equids (*E. hydruntius*) and mainland mammals. Presence of carnivorous. The mammals are similar to the fauna of the South of Italy		R	Cricetidae	*Microtus* (*Terricola*) ex. gr. *savii*	?							?		Literature: 1, 3, 8. Some authors: *Microtus* (*Terricola*) *savii* (6,9,16). Present in the extant fauna. Not endemic. Fossorial (2)
		I	Erinaceidae	*Erinaceus* cf. *europaeus*	Previous FC		?							Literature: 1, 8. For some authors: *Erinaceus europaeus* (9,16) or *Erinaceus* aff. *europaeus* (3). Occurrence uncertain in this FC. Not endemic. It is present in the extant fauna
		I	Soricidae	*Crocidura* cf. *sicula sicula*	*C. sicula esuae* (8)		?							Literature: 1, 3, 8, 9, 16. For some authors: *Crocidura sicula sicula* (6). Endemism. In the extant fauna
		A	Suidae	*Sus scrofa*	Previous FC							X		Literature: 1, 8, 9
		A	Bovidae	*Bos primigenius siciliae*	Previous FC				G					Literature: 1, 3, 8, 9. Endemic
		A	Cervidae	*Cervus elaphus siciliae*	Previous FC				MF					Literature: 1, 3, 8, 9. Endemic
		PR	Elephantidae	*Palaeoloxodon mnaidriensis*	Previous FC				MF /B					Literature: 1, 3, 6, 8, 9, 16. Endemic
		P	Equidae	*Equus hydruntinus*	*E. hydruntinus*				G					Literature: 1, 3, 5, 6, 8, 9, 16. Normal BS
		C	Hyaenidae	*Crocuta crocuta* cf. *spelaea*	Previous FC	X							X	Literature: 1, 3, 8. For some authors: *Crocuta crocuta spelaea* (9)
		C	Canidae	*Vulpes vulpes*	*V. vulpes*	X								Literature: 1, 3, 8, 9. Not endemic
		C	Canidae	*Canis* cf. *lupus*	Previous FC	X								Literature: 1, 8. For some authors: *Canis lupus* (3,9)
		C	Ursidae	*Ursus* cf. *arctos*	Previous FC							X		Literature: 1, 3, 8. For some authors: *Ursus arctos* (9)
		In this FC, some authors (1,2,9) also described *Lepus europaeus* (Lagomorpha, Leporidae), *Bison priscus siciliae* (Artiodactyla, Bovidae) and *Dama carburangelensis* (Artiodactyla, Cervidae)												
Castello FC	0,02 Mya	R	Muridae	*Apodemus* cf. sylvaticus	Previous FC							?		Literature: 3, 9. For some authors: *Apodemus* sp. (1,8)
Island separated by a narrow sea (1). Non-endemic fauna,		R	Cricetidae	*Microtus* (*Terricola*) ex. gr. *savii*	Previous FC							?		Literature: 1, 3, 8. For some authors: *Microtus savii* (9)

low diversity than previous FC, impoverished, unbalanced. The FC is very similar to the fauna of the South of Italy. Arrival by pendal route or land bridge. Faunal exchanges become easier. Presence of *Homo sapiens*		I	Erinaceidae	*Erinaceus europaeus*	Previous FC		?							Literature: 1, 3, 8, 9. Not endemic
		I	Soricidae	*Crocidura* cf. *sicula sicula*	Previous FC		?							Literature: 1, 3, 8, 9. Endemic
		L	Leporidae	*Lepus europaeus*	*L. europaeus*			?						Literature: 1, 3, 8, 9
		A	Suidae	*Sus scrofa*	Previous FC							X		Literature: 1, 3, 8, 9, 16
		A	Cervidae	*Cervus elaphus*	*C. elaphus*				MF					Literature: 1, 3, 5, 8, 9, 16. Normal BS
		A	Bovidae	*Bos primigenius*	*B. primigenius*				G					Literature: 1, 3, 5, 8, 9, 16. Normal BS
		P	Equidae	*Equus hydruntinus*	Previous FC				G					Literature: 1, 3, 5, 8, 9, 16. Normal BS
		P	Equidae	*Equus ferus*	*E. ferus*				G					Literature: 1, 5, 8. For some authors: *Equus ferus* (3). Normal BS
		C	Canidae	*Canis lupus*	Previous FC	X								Literature: 1, 3, 8, 9, 16
		C	Canidae	*Vulpes vulpes*	Previous FC	X								Literature: 1, 3, 8, 9, 16. Prey on small mammals
		In this FC, some authors (9, 16) also described *Mustela* cf. *nivalis* (Carnivora, Mustelidae), *Martes* sp. (Carnivora, Mustelidae), *Lynx lynx* (Carnivora, Felidae) and *Ursus arctos* (Carnivora, Ursidae)												
Transition Castello - Holocene FC	Holocene 0,011 Mya	R	Muridae	*Apodemus* cf. *sylvaticus*	Previous FC							?		Literature: 9
Non-endemic fauna. Pendel route		R	Cricetidae	*Microtus* (*Terricola*) cf. *savii*	Previous FC							?		Literature: 9
		I	Erinaceidae	*Erinaceus europaeus*	Previous FC		?							Literature: 9
		I	Soricidae	*Crocidura* cf. *sícula*	Previous FC		?							Literature: 9
		L	Leporidae	*Oryctolagus cuniculus*	Previous FC			?						Literature: 9
		A	Suidae	*Sus scrofa*	Previous FC							X		Literature: 9
		A	Bovidae	*Bos primigenius*	Previous FC				G					Literature: 9
		A	Cervidae	*Cervus elaphus*	Previous FC				MF					Literature: 9
		A	Cervidae	*Capreolus capreolus*										Literature: 9. Occurence uncertain
		P	Equidae	*Equus hydruntinus*	Previous FC				G					Literature: 9
		C	Mustelidae	*Martes* sp.	*Martes* sp.	X								Literature: 9
		C	Mustelidae	*Mustela* cf. *nivalis*	*M. nivalis*	X								Literature: 9
		C	Canidae	*Canis lupus*	Previous FC	X								Literature: 9
		C	Canidae	*Vulpes vulpes*	Previous FC	X								Literature: 9
		C	Felidae	*Felis silvestris*	*F. silvestris*	X								Literature: 9

Holocene FC	Early Holocene 0,01 MyA	R	Muridae	*Apodemus* cf. *sylvaticus*	Previous FC							?		Literature: 9. For some authors: *Apodemus sylvaticus* (8)
		R	Cricetidae	*Microtus* (*Terricola*) *savii*	Previous FC							?		Literature: 9. For some authors: *Microtus* (*Terricola*) cf. *savii* (8)
		R	Cricetidae	*Arvicola terrestris*	*A. terrestris*							?		Literature: 8, 9
		R	Gliridae	*Glis glis*	*G. glis*							?		Literature: 9. = *Myoxus glis* (8)
		I	Erinaceidae	*Erinaceus europaeus*	Previous FC		?							Literature: 8, 9
		I	Soricidae	*Crocidura* cf. *sicula sicula*	Previous FC		?							Literature: 9. For some authors: *Crocidura* sp. (8)
		L	Leporidae	*Oryctolagus cuniculus*	Previous FC			?						Literature: 9
		Q		*Chiroptera* indet.										Literature: 8
		A	Suidae	*Sus scrofa*	Previous FC							X		Literature: 8, 9
		A	Cervidae	*Cervus elaphus*	Previous FC				MF					Literature: 9. For some authors: *Cervus* sp. (8)
		A	Bovidae	*Bos primigenius*	Previous FC				G					Literature: 8, 9
		P	Equidae	*Equus hydruntinus*	Previous FC				G					Literature: 9
		C	Mustelidae	*Lutra lutra*	*L. lutra*	X								Literature: 9
		C	Mustelidae	*Martes* sp.	Previous FC	X								Literature: 8, 9
		C	Mustelidae	*Mustela* cf. *nivalis*	Previous FC	X								Literature: 8, 9
		C	Canidae	*Canis* (cf.) *lupus*	Previous FC	X								Literature: 8, 9
		C	Canidae	*Vulpes vulpes*	Previous FC	X								Literature: 8, 9
		C	Felidae	*Felis silvestris*	Previous FC	X								Literature: 8, 9
		C	Ursidae	*Ursus* sp.	Previous FC							X		Literature: 8
		C	Phocidae	*Monachus monachus*	*M. monachus*	X								Literature: 8

These charts follow the FC distribution known classically (Bonfiglio et al. 2002, Masini et al. 2008), see Marra (2013) for a new proposal of biochronological organization based on the large mammals of Sicily. Bibliographic legend: (1) Marra 2005, (2) Marra 2013, (3) Palombo 2007, (4) Alcover et al. 1981, (5) Sondaar and Van der Geer 2005, (6) Van der Geer et al. 2010, (7) Hunt and Schembri 1999, (8) Bonfiglio et al. 2002), (9) Masini et al. 2008, (10) Daams and De Bruijn 1995, , (11) Thaler (1972), (12) Fladerer and Fiore 2003, (13) Lyras et al. 2010, (14) Burgio and Fiore 1997, (15) Bonfiglio 1992, (16) Palombo 2009a, (17) Dubey et al. 2008, (18) Hutterer 1991, (19) Lister and Bahn 1994, (20) Ambrosetti 1968, and (21) Abbazzi et al. 2001.

7. MALTA

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
Elephas falconeri FC	Early Middle Pleistocene 0.9 Mya	R	Gliridae	*Leithia melitensis*	*Leithia* Monte Pellegrino (1)							?		Literature: 1, 2. Endemic
Unbalanced and partly endemic. Site: older layer of the Zebbug fissure		R	Gliridae	*Leithia cartei*	*Leithia* Monte Pellegrino (1)							?		Literature: 2, 3. Endemic
		R	Gliridae	*Maltamys gollcheri*	*Leithia* Monte Pellegrino (1)							?		Literature: 1, 3. = *Eliomys gollcheri* (3). Endemic. Smaller than *Leithia*
		I	Soricidae	*Crocidura sicula esuae*	(?) *C. tarfayaensis* (4)		?							Literature: 1,2. = *C. esuae* or *esui* (5). Endemic. Larger BS. Uncertain origin, probably from North Africa (4)
		PR	Elephantidae	*Palaeoloxodon falconeri*	*P. antiquus*				MF /B					Literature: 1, 2, 3. Endemic. Strongly reduced in BS, dwarf (90 cm at shoulders). BM=100-170kg. It is also suggested a *Mammuthus* origin (6). Initially, it is described *P. melitensis* that is just the larger form of this sexually dimorphic species (7)
		C	Mustelidae	*Lutra euxena*	*L. simplicidens*	X								Literature: 1. = *Nesolutra euxena* (8). Exclusively from Malta
		In this FC, some authors (1,2,3) also described *Maltamys wiedincitensis* (Rodentia, Gliridae), *Hippopotamus pentlandi* (Artiodactyla, Hippopotamidae) and *Vulpes* sp. (Carnivora, Canidae), but the occurrence is uncertain												
Elephas mnaidriensis FC	Late Middle Pleistocene to Early Late Pleistocene 0.3 Mya	R	Gliridae	*Leithia cartei*	Previous FC							?		Literature: 1. Endemic
Endemism, impoverished and unbalanced. Oversea dispersal from Sicily or connections (strong filter). Mainly it is characterized by herbivores and large dormice. The main difference with Sicilian		R	Gliridae	*Maltamys gollcheri*	Previous FC			X						Literature: 1. Endemic. Smaller than *Leithia*
		R	Gliridae	*Maltamys wiedincitensis*	Previous FC							?		Literature: 1. Endemic. Smaller than *Leithia*
		I	Soricidae	*Crocidura sicula esuae*	Previous FC		?							Literature: 1, 2. Endemic

fauna is the smaller BS of the hippopotamus and elephant in combination with a larger degree of endemism. Sites: Ghar Dalam, Crendi, Mnajdra Gap, Mellieha and younger layer of Zebbug fissure		PR	Elephantidae	*Palaeoloxodon mnaidriensis*	*P. antiquus*				MF /B					Literature: 1, 2, 3
		A	Hippopotamidae	*Hippopotamus melitensis*	*H. pentlandi* or a previous dispersion (2)				G					Literature: 1, 2. Smaller than *H. pentlandi* (Sicily)
		C	Mustelidae	*Lutra euxena*	Previous FC	X								Literature: 1, 9, 10 = *Nesolutra euxena* (8)
		Q		Bats										Literature: 1, 3
		In this FC, some authors (2,3) also described *Canis lupus* (Carnivora, Canidae), *Ursus* cf. *arctos* (Carnivora, Ursidae), *Vulpes* sp. (Carnivora, Canidae), *Cervus elaphus siciliae* (Artiodactyla, Cervidae), *Pitimys melitensis* (Rodentia, Cricetidae), *Equus* sp. (Perissodactyla, Equidae), *Sus* sp. (Artiodactyla, Suidae) and *Bos* sp. (Artiodactyla, Bovidae).											
Cervus sp. FC	Late Pleistocene	R	Gliridae	*Leithia cartei*	Previous FC							?		Literature: 1. Endemic
Isolated from the Sicily. Strong filter between the two islands. It has a large degree of endemism. Site: Ghar Dalam		R	Gliridae	*Maltamys gollcheri*	Previous FC							?		Literature: 1. Smaller than *Leithia*. Endemic
		R	Gliridae	*Maltamys wiedincitensis*	Previous FC							?		Literature: 1. Smaller than *Leithia*. Endemic
		R	Cricetidae	*Microtus* (*Terricola*) *melitensis*	?							?		Literature: 1, 9. = *Pitymys melitensis* (11). It is also described another species *P. pauli* not encountered much in the literature. Endemic
		I	Soricidae	*Crocidura* sp.	?		?							Literature: 1, 9. Endemic
		A	Cervidae	*Cervus* sp.	*C. elaphus*				G					Literature: 1, 9. Sometimes referred to as a fallow deer (*Dama dama*) or as the red deer from Sicily (*Cercus elaphus siciliae*). Endemic. Slightly reduced in BS
The extinction of this fauna may have been caused by a volcanic event. Later, during the Holocene, new micromammals arrived from the mainland (*Suncus etruscus*, *Crocidura* cf. *leucodon*, *Crocidura russula*, *Ursus* cf. *arctos*, *Cervus* cf. *elaphus* and domestic animals) (1)													

Malta is connected to Sicily during the Late Miocene. At the onset of the Pliocene, Malta became isolated. The submerged ridge that connected Malta and Sicily is supposed to have been partly exposed with sea-level falls. In such a way, during the Early to middle Middle Pleistocene some FC of Sicily colonized Malta. Since that period, the island horboured its own endemic fauna. The endemics evolved from Sicilian taxa through vicariance effects (1). The main site is Ghar Dalam. Bibliographic legend: (1) Van der Geer et al. (2010), (2) Marra 2005, (3) Hunt and Schembri (1999), (5) Hutterer 1991, (4) Dubey et al. 2008, (6) Lister and Bahn 1994, (7) Ambrosetti 1968, (8) Willemsen 2006, (9) Alcover et al. 1981, (10) Lyras et al. 2010, and (11) Chaline et al. 1999.

8. PITYUSIC ISLANDS (EIVISSA, FORMENTERA AND NEARLY 60 SMALLER SURROUNDING ISLETS)

FAUNAL COMPLEX	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/ RELATIVE	DIET								MORE INFORMATION
						C	I	H	HFO	HFR	HGR	O	N	
Ses Fontenelles FC	(?) Late Miocene-Early Pliocene (1)	R	Gliridae	*Eliomys* sp.	*Eliomys* sp.							?		Literature: 2
The earliest insular fauna from Eivissa. Its statigraphic position is not known		R	Gerbillidae	*Protatera* sp.	?							?		Literature: 2
		L	Leporidae	*Hypolagus balearicus*	?			?						Literature: 2, 3. Endemic. BM=1.3-2.7kg
		A	Bovidae	Bovidae sp. 1	?			?						Literature: J. Quintana (personal comment). Previously attributed to *Tyrrhenotragus* sp. (2)
		A	Bovidae	Bovidae sp. 2	?			?						
Cova de Na Reia FC	Late Pliocene (1)	R	Gliridae	*Eliomys* (*Eivissia*) *canarreiensis*	*Eliomys*							?		Literature: 1, 4, 5. Endemic
Fossil record extremly poor. This FC extincted as a result of one natural disaster of unknown origin		R	Gliridae	*Eliomys* sp.	*Eliomys*							?		Literature: 1, 4, 5. Endemic
Birds and Bats FC	Late Pleistocene	The fauna is only composed by flight vertebrates (birds and insectivorous bats) and a lacertid lizard (*Podarcis pityusensis*). Eight Late Pleistocene deposits are known from Eivissa and Fromentera concerning this period												
Its extinction would be relate to a dramatic event, such as a volcanic episode (1)														

The two main islands (Eivissa and Formentera) are separated by a narrow and shallow channel. During all their paleogeographical history, they shared their faunas. Bibliographic legend: (1) Bover and Alcover (2008), (2) Bover et al. 2008, (3) Quintana and Moncunill-Solé 2014, (4) Sondaar and Van der Geer 2005, and (5) Marra 2005

9. SMALL ISLANDS

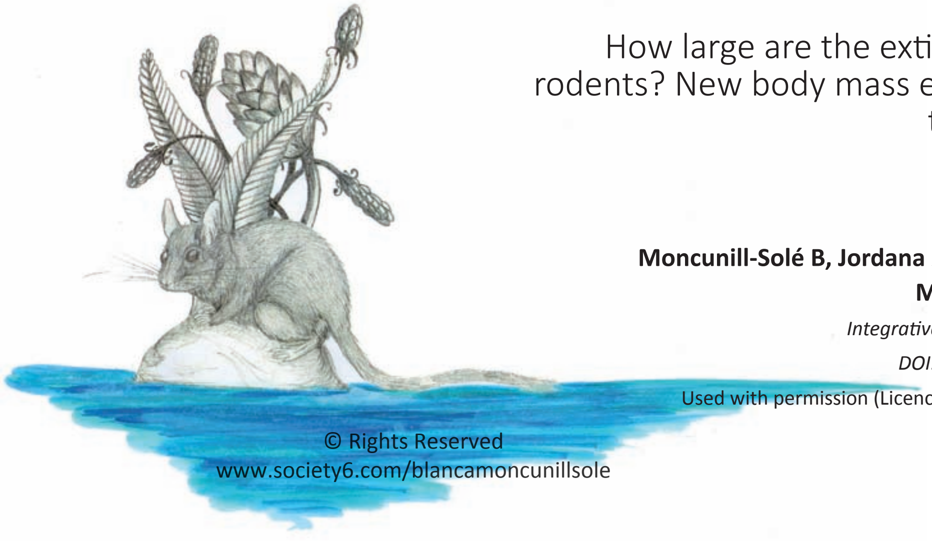
ISLAND	GEOLOGICAL AGE	ORDER	FAMILY	SPECIES	ANCESTOR/RELATIVE	MORE INFORMATION
KARPATHOS AND KASOS	Plio-Quaternary	A	Cervidae	*Praemegaceros* (*Candiacervus*) *cerigensis*	*P. verticornis*	Literature: 1, 2. Descendent of Creta. The first one is of small BS and the latter of medium BS. Mixed feeders
		A	Cervidae	*Praemegaceros* (*Candiacervus*) *pigadiensis*		
		R	Muridae	*Mus* sp.	?	Literature: 2. Late Pleistocene of Karpathos
		R	Muridae	*Mesocricetus rathgeberi*	?	Literature: 2. Holocene. Armathia islet, Kasos
PALAEOCYCLADES (NAXOS, DELOS, PAROS, SERIPHOS, MILOS)	Late Pleistocene	PR	Elephantidae	*Palaeoloxodon lomolinoi*	*P. antiquus*	Literature: 2, 3. Dwarf (10% of *P. antiquus*). Several species. Probably more browser
		I	Soricidae	*Crocidura* sp.	?	Literature: 2, 3.
		R	Muridae	*Apodemus* cf. *mystacinus*	?	Literature: 2, 3. Late Pleistocene. Large BS
		C		Bats		Literature: 2
AMORGÓS	Plio-Quaternary	A	Cervidae	Similar to *C. cretensis*	?	Literature: 2. Dwarf
		?		Micromammals indet.		Literature: 2
TILOS	Late Late Pleistocene to Holocene	A	Cervidae	Indet (*Dama dama*)	?	Literature: 2, 4. Endemic. First fauna (extinction at 140000 years before present)
		PR	Elephantidae	*Palaeoloxodon tiliensis*	*P. antiquus*	Literature: 2, 4, 5. Dwarf (50% smaller than *P. antiquus*). Agile. Mixed feeder. Following cervid fauna, its arrival to Tilos was probably 50000 years before present
		Q	Vespertilionidae	*Myotis blythii*	?	Literature: 2. With elephant remains
		C	Ursidae	*Ursus arctos*	?	Literature: 2
RHODOS	Plio-Quaternary	PR	Elephantidae	Indet.	*P. antiquus*	Literature: 2. Dwarf. Mixed feeder
		A	Cervidae	*Cervus* sp.	?	Literature: 2. Associated to a mainland fauna

CAPRI	Late Pleistocene	A	Cervidae	*Cervus elaphus tyrrhenicus*	*C. elaphus*	Literature: 1, 2. = *Cervus tyrrhenicus*. Endemic. Mixed feeder
		R	Muridae	*Apodemus sylvaticus tyrrhenicus*	?	Literature: 1, 2. Endemic. Large BS
		R	Gliridae	*Muscardinus malatestai*	?	Literature: 1
	Middle-Late Pleistocene (balanced fauna)	C	Felidae	*Panthera pardus*	?	Literature: 1
		C	Canidae	*Canis* sp.	?	Literature: 1
		C	Ursidae	*Ursus spelaeus*	?	Literature: 1
		P	Rhinocerotidae	*Dicerorhinus* cf. *hemitoechus*	?	Literature: 1
		P	Equidae	*Equus* sp.	?	Literature: 1
		A	Suidae	*Sus scrofa*	?	Literature: 1
		A	Hippopotamidae	*Hippopotamus amphibus*	?	Literature: 1
		A	Bovidae	*Bos primigenius*	?	Literature: 1
		PR	Elephantidae	*Mammuthus chosaricus*	?	Literature: 1
		PR	Elephantidae	*Elephas antiquus*	?	Literature: 1. Uncertain occurence
		A	Cervidae	*Cervus dama*	?	Literature: 1
		A	Cervidae	*Cervus elaphus*	?	Literature: 1
PIANOSA	Unknown	A	Bovidae	*Bos primigenius bubaloides*	*B. primigenius*	Literature: 1. Grazer
		A	Cervidae	*Cervus*	?	Literature: 1
		A	Cervidae	*Cervus elaphus*	?	Literature: 1
		C	Mustelidae	*Mustela* sp.	?	Literature: 1. Pleistocene
		P	Equidae	*Equus hydruntinus*	?	Literature: 1
ELBA	Middle to Late Pleistocene. Balanced fauna	A	Cervidae	*Cervus elaphus*	*C. elaphus*	Literature: 1. Similar to mainland species

Literature: (1) Petronio 1990, (2) Alcover et al. 1981, (3) Van der Geer et al. 2014, (4) Palombo 2007, and (5) Thedorou et al. 2007

Chapter 4

How large are the extinct giant insular rodents? New body mass estimations from teeth and bones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ORIGINAL ARTICLE

How large are the extinct giant insular rodents? New body mass estimations from teeth and bones

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Abstract

The island rule entails a modification of the body size of insular mammals, a character related with numerous biological and ecological variables. From the Miocene to human colonization (Holocene), Mediterranean and Canary Islands were unaltered natural ecosystems, with paleofaunas formed with endemic giant rodents among other mammals. Our aim is to create methods to estimate the body masses of fossil island rodents and address the nature of ecological pressures driving the island rule. We created regression equations based on extant rodent data and used these to estimate the body masses of the extinct species. Our results show strong correlations between teeth, cranial and postcranial measurements and body mass, except for the length of the long bones, the transversal diameter of the distal tibia and the anteroposterior diameter of the proximal tibia, where the equations were less reliable. The use of equations obtained from a more homogeneous group (suborder and family) is preferable when analyzing the area of the first molar. The new regressions were applied to estimate the body masses of some Mediterranean and Canarian fossil rodents (*Canariomys*, *C. bravoi* 1.5 kg and *C. tamarani* 1 kg; *Hypnomys*, *H. morpheus* 230 g and *H. onicensis* 200 g; and *Muscardinus cyclopeus* 100 g). Our results indicate that under absence of predation, resource availability (island area) is the key factor that determines the size of the *Canariomys* sp. However, under presence of specialized predators (birds of prey), body size evolution is less pronounced (*Hypnomys* sp.).

Key words: body mass, *Canariomys*, *Hypnomys*, island rule, *Muscardinus cyclopeus*

INTRODUCTION

Islands are evolutionary and ecological units. Their distinctive features (geographic limitations, limited primary productivity, reduced number of species and low biodiversity, absence of mammalian predators and overall lower predation pressure, diversity and intensity of the ecological interactions, degree of isolation and geo-

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logical age) make each island an extraordinary natural laboratory (MacArthur & Wilson 1967; Whittaker 1998; McNab 2002; Millien *et al.* 2006), thus offering a series of repeatable and, hence, testable experiments. As a consequence of isolation, insular endemics are under selective pressures that importantly differ from those on the mainland entailing noticeable changes in morphological and other traits (Lomolino 2005; Lomolino *et al.* 2012). One of the most important tendencies is the modification of body size in mammals, coined the 'island rule' (van Valen 1973). It describes the tendency towards gigantism in small mammals and dwarfism in large ones (Foster 1964; van Valen 1973; Lomolino 1985, 2005). The evolution and variation of mammalian body size is a most interesting topic because it affects a multitude of biological attributes of the animal: immigration potential, home range, ecological interactions, behavioral adaptations, locomotion, body composition, brain size, resources requirements, diet, basal metabolic rate, demography and life history traits (e.g. growth rate, lifespan, litter size, survivorship, age at weaning and torpor) (Calder 1984; Damuth & MacFadden 1990; Brown *et al.* 1993; McNab 1994, 2002, 2010; Köhler & Moyà-Solà 2001, 2004, 2009; Bromage *et al.* 2002; Raia *et al.* 2003; Lomolino 2005; Köhler 2010; Jordana & Köhler 2011; Marín-Moratalla *et al.* 2011). Since the first description of the island rule, a series of studies of current island faunas have been performed with the aim of shedding light on this particular issue (Heaney 1978; Lomolino 1985, 2005; Anderson & Handley 2002; Michaux *et al.* 2002; Meiri *et al.* 2005, 2008; McNab 2010). The extinct endemic faunas (composed of small and large mammals, like elephants, hippopotamus or bovids) are unaltered by humans (McNab 2002) and, hence, are considered to be key to understanding the island rule. Nevertheless, studies on body size changes in these paleofaunas are quite rare (Biknevicius *et al.* 1993; Raia & Meiri 2006; Palombo 2009).

The order Rodentia, the most diversified order of extant Mammalia (Wilson & Reeder 2005), was particularly well represented in past insular faunas with genera and species that are extinct today (Millien *et al.* 2006). The giant rodents from the mainland paleofauna of South America have been studied in detail and estimations of their body masses have been provided (Sánchez-Villagra *et al.* 2003; Hopkins 2008; Millien 2008; Rinderknecht & Blanco 2008; Millien & Bovy 2010). Nevertheless, body masses (the best proxy of body size [Gingerich *et al.* 1982; Jungers 1990; Biknevicius *et al.* 1993]) of rodents from Miocene through Pleistocene of the Mediterranean Islands and Canary Islands are only poorly known. Most of the genera and species found on these islands were endemisms (e.g. *Hypnomys* sp., *Hattomys* sp., *Mikrotia* sp., *Stertomys* sp., *Maltamys* sp. and *Canariomys* sp.) characterized by a spectacular body size increase and remarkable morphological and behavioral modifications (e.g. locomotion and diet) (Fig. 1) (Freudenthal 1971; López-Martínez & López-Jura-

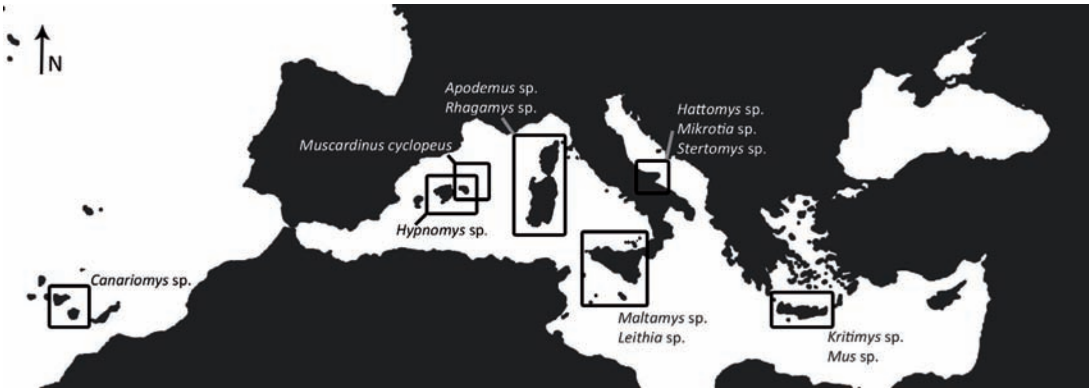

Figure 1 Diagram of Mediterranean and Canary Islands with the most important genera of rodents from Miocene through Holocene. *Canariomys* sp. from the Canary Islands; *Hypnomys* sp. from Balearic Islands; *Muscardinus cyclopeus* from Minorca; *Apodemus* sp. and *Rhagamys* sp. from Sardinia and Corsica; *Hattomys* sp., *Mikrotia* sp. and *Stertomys* sp. from Gargano; *Maltamys* sp. and *Leithia* sp. from Sicily and Malta; and *Kritimys* sp. and *Mus* sp. from Crete. (See text for references.)

do 1987; Bonfiglio *et al.* 2002; Marra 2005; Sondaar & van der Geer 2005; Palombo 2006; Masini *et al.* 2008). Here, we focus on fossil rodents showing striking increase in body size: *Canariomys* sp., *Hypnomys* sp. and *Muscardinus cyclopeus* Agustí, Moyà-Solà and Pons-Moyà, 1982 (Fig. 1).

Canariomys is the extinct rodent genus from the Canary Islands (Spain), represented by 2 species: *Canariomys bravoi* Crusafont-Pairó, 1964 (Tenerife) and *Canariomys tamarani* López-Martínez & López-Jurado, 1987 (Gran Canaria). It is related to the African murids (*Pelomys* sp. and *Arvicanthis* sp.), whose last common ancestor lived during the Miocene–Pliocene transition. Studies of microwear and morphology suggest an herbivorous diet excluding grasses, terrestrially and an increase in digging capacity, relating it to a relatively damp, open habitat with herbaceous vegetation (López-Martínez & López-Jurado 1987; Firmat *et al.* 2010; Michaux *et al.* 2012). Its coexistence with the first native human population contributed, either directly or indirectly, to its extinction (Michaux 2008; Morales *et al.* 2009). *Hypnomys* is an extinct genus from the Gymnesian Islands (Majorca and Minorca, Spain). It evolved in isolation for at least 5.35 Myr, from the Messinian Crisis when the ancestor entered from the mainland to the Late Pleistocene–Holocene. Five different chronospecies are identified: *Hypnomys waldreni* Reumer, 1979 (Late Pliocene), *Hypnomys onicensis* Reumer, 1994 (Early to Middle Pleistocene) and *Hypnomys morpheus* Bate, 1918 (Late Pleistocene) from Majorca; and *Hypnomys eliomyoides* Agusti, 1980 (Late Pliocene–Pleistocene) and *Hypnomys mahonensis* Bate, 1919 (Late Pleistocene) from Minorca (Marra 2005; Sondaar & van der Geer 2005). Its closest relative is considered to be the extant garden dormouse (*Eliomys* sp.) (Bover *et al.* 2008). It was a terrestrial rodent with fossorial activities (Bover *et al.* 2010) and an omnivorous diet that included hard items (Hautier *et al.* 2009). It went extinct during the Late Holocene with the arrival of humans on the islands (Alcover & Roca 1975; Bover & Alcover 2008). *Muscardinus cyclopeus* is a Late Miocene to Middle/Late Pliocene rodent species endemic from Minorca (Spain); the genus itself *Muscardinus* is not endemic. Its extinction coincides with the *Myotragus* paleofauna invasion in Late Pliocene to Early Pleistocene when Majorca and Minorca were connected (Bover *et al.* 2008). Little more is known from this giant dormouse.

Few studies for estimating the body masses of these 3 genera of rodents have been performed. López-Martínez and López-Jurado (1987) calculate a body mass of 750–1200 g for *C. tamarani*. In contrast, Michaux *et al.* (1996) provide body masses for *C. bravoi* between 1900 and 2300 g and for *C. tamarani* 1350 g. Michaux *et al.* (2012) estimate body masses of approximately 1 kg for the 2 species of *Canariomys* (particular skeletons). Bover *et al.* (2010) estimate the body mass of an articulated specimen of *H. morpheus* as between 173 and 284 g. No estimation has hitherto been performed for *M. cyclopeus*.

Allometric regressions of body mass on dental, cranial and postcranial parameters for extant rodents are a method for reconstructing the average weight of extinct species (Legendre 1986; Damuth & MacFadden 1990; Biknevicius *et al.* 1993; Parra & Jaeger 1998; Reynolds 2002; Hopkins 2008; Millien & Bovy 2010). Our interest focuses on island species, which had a particular evolution as a consequence of the specific ecological habitat where they lived (Palkovacs 2003; Lomolino *et al.* 2012). However, dental and cranial parameters of dwarf insular mammals do not follow the scaling pattern of their normal-sized relatives. Our principal aim is to create methods for estimating body masses of extinct rodents and to calculate and test the body mass estimations of *Canariomys* sp., *Hypnomys* sp. and *M. cyclopeus*, thus contributing to our understanding of the island rule. The results obtained for these 3 insular genera will shed light on the controversy on the allometry of teeth, cranial and postcranial traits. *Oreopithecus bambolii* Gervais, 1872, for instance, presents a tooth size much smaller than expected from postcranial dimensions (Moyà-Solà & Köhler 1997).

MATERIALS AND METHODS

The taxonomy used in the current paper follows Wilson and Reeder (2005).

Database

Data for extant individuals of rodents were collected from 58 wild species included in 14 families (Table S1), maximizing the taxonomic diversity and minimizing the effects of phylogeny (Mendoza *et al.* 2006); 18 species are insular. Splitting the sample into different groups according to their origin (i.e. New or Old World, and island or mainland) has not had significant results and for this reason we analyzed all the data as a sole group. The range of body sizes is very broad, from 40 kg for *Hydrochaeris hydrochaeris* Linnaeus, 1766 to 15 g for *Mus musculus* Linnaeus, 1758, covering the evolutionary diversity of the order and, *ergo*, is appropriate for body mass estimation of giant insular rodents. The collections come from Rijksmuseum van Natuurlijke Historie of Leiden (RMNH), Universitat de Barcelona (UB), Universitat de les Illes Balears (UIB) and Museo de Ciencias Naturales de Madrid (MCNM). For some taxa postcranial data were not available and these taxa were excluded from the analysis. Data for teeth were complemented with data from the published literature (Legendre 1989).

The fossil material comprises 5 species: *C. bravoi*, *C. tamarani*, *H. onicensis*, *H. morpheus* and *M. cyclopeus*. The collections are housed in the Institut Català de Paleontologia Miquel Crusafont (ICP) (*C. bravoi*, *H. morpheus* and *H. onicensis*) and in the 'Col·lecció Bep Quintana' (Ciutadella de Menorca) (*M. cyclopeus*); some data were recovered from the published literature (*C. bravoi* and *C. tamarani*) (López-Martínez & López-Jurado 1987; Blanco 2005).

Measurements

For each specimen, a set of parameters was measured. The following measurements were taken on the postcranial material: humerus length (HL), femur length (FL), pelvis length (PL), cubit length (CL), tibia length (TL), proximal humeral anteroposterior diameter (HAPDp), distal humeral anteroposterior diameter (HAPDd), distal humeral transversal diameter (HTDd), proximal femoral transversal diameter (FTDp), distal femoral anteroposterior diameter (FAPDd), distal femoral transversal diameter (FTDd), proximal tibia anteroposterior diameter (TAPDp), proximal tibia transversal diameter (TTDp) and distal tibia transversal diameter (TTDd). In the case of the cranium and teeth, the following measurements were taken: the width of occipital condyle (WOC), the maximum length of the first lower molar (LM/1), the maximum width of the first lower molar (WM/1), the length of the maxillary toothrow (TRL) and the width of the first upper molar (WM1/). The measurements are defined in Cabrera (1980), Köhler and Moyà-Solà (2004), Blanco (2005) and Hopkins (2008). Two types of instruments were used to take the measures: a digital electronic precision caliper (0.05 mm error) and the Nikkon Measuroscope 10. In some cases, the body mass (BM) is recorded in the collections; in the cases where it was not specified, we gathered the data from the published literature (Silva & Downing 1995; Ernest 2003; more references in Table S1). The average of multiple individuals was used to create the model (Table S1), in order to not confuse intraspecific and interspecific allometry.

Statistical analyses

The models used to estimate the body masses of extinct animals were allometric, expressed as a power function $Y = aX^b$ [where a is a constant, b is the allometric coefficient, X the independent variable (values from teeth or bone) and Y is the estimated variable (body mass)]. The power function was log transformed, obtaining a linear relationship ($\log Y = \log a + b \log X$ in the bivariate case and $\log Y = \log a + b_1 \log X_1 + b_2 \log X_2 + ... + b_k \log X_k$ in multiple ones). The data were fitted by the method of least squares (Smith 1980). In all cases, we assumed the suppositions of the linear regression model (i.e. random sample, normal distribution of the variables and homogeneity of variances). Previously, the data were converted into cubic and square roots (depending on whether the measurement was volume or area) to scale the results. The homogeneity of the residuals was controlled through residuals *versus* predicted graphics and Cook's distance (D_i). The species with residuals far from the general tendency and large D_i were eliminated and the model was reconstructed again. To evaluate the precision and adjustment of the allometric models, we calculated: the coefficient of determination, r^2; the standard error of the estimate, SEE (= $\sqrt{\text{RMS}}$ or $\sqrt{\text{Residual Mean Square}}$); the average absolute percent prediction error, %PE (= [(observed – predicted) / predicted] × 100); and the mean absolute percent prediction error, MAPE ($= \frac{100}{n} \sum_{t=1}^{n} |(y_t - \hat{y}_t)/y_t|$) (Smith 1980, 1984). To test the resultant equations, validations of them were carried out. In the case of simple regressions, some genera were removed and a new equation was performed without these data. We observed whether the percentage of error (predicted *versus* observed) was inside the 50% of seasonal variation typical of rodents (Pelzer *et al.* 1999; Rosário & Mathias 2004; Rana *et al.* 2006). In the case of multiple regressions (cranial, humerus, femur and skeleton), we performed cross-validation tests. For each species a new equation was obtained excluding the species' data. Thus, we obtained predicted (from the equation without the species' data) and observed (real) values for each species. Correlations between predicted and observed scores informed us about the suitability of the equations. When the body mass estimation regression models were applied to the fossil register, the results were corrected by a logarithmic correcting factor. The detransformed predicted values of each equation (values of body mass) were multiplied by Ratio Estimation (RE = $\bar{y} / \bar{z}$, where y_i is the observed value of the dependent variable y for the ith observation on the original measurement scale and z_i is the predicted value for the ith observation, detransformed back to the original measurement scale without correction) (Smith 1993). We calculated the body mass for each specimen and then performed the average and confident intervals (IC = $\bar{X} \pm \frac{\sigma}{\sqrt{n}} z_{\alpha/2}$) of each specific measurement. Based on body mass results for each equation, we calculated a simply average ($\bar{X}$) (Scott 1990; Mendoza *et al.* 2006), a geometric mean ($\bar{X}_G$) and a weighted mean ($W_M = \sum_{M_i}^{1}((\frac{M_i}{\%PE}) \times \sum_{M_i}^{1} \%PE) \times n^{-2}$) (Christiansen & Harris 2005). The analyses were performed using the IBM SPSS Statistics 19 software following the references of Pérez (2001).

When sufficient samples were available (cranial and dental), additionally to the regression with 'all rodent' species, we carried out models for more homogenous groups (suborder and family levels) (Hopkins 2008).

RESULTS

The graphics of all pairwise regression models performed are shown in Fig. S1.

Cranial measurements

Width of occipital condyle (WOC) is a parameter frequently used to predict body masses of large mammals (Martin 1980; MacFadden & Hulbert 1990; Köhler & Moyà-Solà 2004; Palombo *et al.* 2008), but it is not used for small mammals. Simple regressions including all the taxa show significant results, $r^2 = 0.953$ ($P < 0.05$) (Table 1). *Papagomys armandvillei* Jentink, 1892 was excluded from the model because is far from the general tendency of the other species (residues *versus* predicted graphics) and has the largest Cook's distance ($D_i = 0.2$). The sample of individuals used for measurements is small (3) and the species' body mass used to create the model is an estimate. Regressions of suborders (Hystricomorpha, Myomorpha and Sciuromorpha) and families (Muridae) were carried out, excluding *Papagomys*. The models had high determination coefficients as well. In all the cases, SEE, %PE and MAPE presented low values and the validations are correct (inside de 50% variation) (Table 1).

Dental measurements

M1 area (M/1AA = LM/1 × WM/1) and toothrow area (TRAA = WM1/ × TRL) are most frequently used to estimate the body mass of mammals, specifically in rodents (Gingerich *et al.* 1982; Legendre 1986; Janis 1990; Hopkins 2008). Our data on the M1 area was supplemented with data from Legendre (1989), using a total of 247 species for the study.

The relationship between $\sqrt[3]{BM}$ and $\sqrt{M/1AA}$ was high and significant ($P < 0.05$), $r^2 = 0.891$. The analyses at the level of suborder and family were significant statistically too ($P < 0.05$) with slight variation in respect to the analysis of the all rodents (Table 1).

The performed simple analysis with TRAA generated a high significant linear model for all rodent taxa ($r^2 = 0.902$) and by suborders and families (Table 1). *P. armandvillei* and *Phloeomys cumingi* Waterhouse, 1839 were eliminated because they are far from the general tendency of the other species (residues *versus* predicted graphics) and have the largest Cook's distances (D_i *P. armandvillei* = 0.13 and D_i *P. cumingi* = 0.7). This can be explained by the small number of individuals used to represent the species (3 and 1, respectively) and the low reliability of body mass values. In both cases, the models were precise (low values of SEE, %PE and MAPE) and the validations correct (inside 50% of variation) (Table 1).

Postcranial measurements

Postcranial material has rarely been used to estimate body masses, although equations for these parameters have been developed (Biknevicius *et al.* 1993; Millien & Bovy 2010). In our analysis, the number of species was reduced to a maximum of 33, varying depending on the parameters used because some of the skeletons were incomplete. We did not consider it appropriate here to perform analyses for each data of suborder and family because of the reduced number of species.

First, simple regressions between the $\sqrt[3]{BM}$ and each of the lengths of the long bones and pelvis (HL, FL, CL, TL and PL) were performed. The models were significant but with lower coefficients of determination than those observed with other parameters (Table 1). Second, pairwise analyses were carried out with the dimensions of the long bones epiphyses (HAPDp, HAPDd, HTDd, FTDp, FAPDd, FTDd, TAPDp, TTDp and TTDd). The coefficient of determination was overall high, especially in the cases of HAPDd, FTDd and TTDp ($r^2 = 0.903$, $r^2 = 0.923$ and $r^2 = 0.902$, respectively) (Table 1).

In all models SEE, %PE and MAPE were very low, except for TTDd and TAPDp. These values were importantly influenced by the small size of the sample (Table 1). The validation test was correct in all the cases, except for CL and FAPDd. Because both considerably exceeded the 50% of variation, we did not consider these in our estimation of rodent body masses.

Multiple analyses

We performed different multiple regressions: ones using parameters of one specific bone/part of body (e.g. humerus or cranium) and others with all variables. In

Table 1 Parameters of interspecific regression equations between body mass and bone measurements (equation: log $\sqrt[3]{\mathrm{BM}} = a + b_1$ log measurement + b_2 log measurement)

Measurement (mm)	a	b_1	b_2	$P < 0{,}05$	r^2	SEE	%PE	MAPE	RE	Comments
WOC (All rodents)	–0.507	1.304		*	0.953	0.055	10.205	5.164	1.008	*Papagomys* sp. not included
WOC (Hystricomorpha)	–0.400	1.246		*	0.951	0.049	8.292	3.166	1.010	
WOC (Myomorpha)	–0.480	1.267		*	0.909	0.060	11.020	6.361	1.007	*Papagomys* sp. not included
WOC (Sciuromorpha)	–0.439	1.234		*	0.981	0.035	6.514	3.147	1.006	
WOC (Muridae)	–0.419	1.193		*	0.927	0.051	9.275	5.511	1.002	*Papagomys* sp. not included
$\sqrt{\text{M/1AA}}$ (All rodents)	0.320	1.130		*	0.891	0.081	14.773	9.750	1.030	
$\sqrt{\text{M/1AA}}$ (Hystricomorpha)	0.439	1.038		*	0.906	0.071	10.495	4.430	1.017	
$\sqrt{\text{M/1AA}}$ (Myomorpha)	0.318	1.051		*	0.850	0.069	11.960	8.240	1.019	
$\sqrt{\text{M/1AA}}$ (Sciuromorpha)	0.355	1.191		*	0.955	0.055	9.897	5.947	1.008	
$\sqrt{\text{M/1AA}}$ (Muridae)	0.314	1.100		*	0.873	0.062	10.460	6.776	1.014	
$\sqrt{\text{TRAA}}$ (All rodents)	0.129	1.042		*	0.902	0.074	13.182	6.575	1.018	*Papagomys* sp. and *Phloeomys* sp. not included
$\sqrt{\text{TRAA}}$ (Hystricomorpha)	0.068	1.100		*	0.865	0.081	13.133	5.829	1.019	
$\sqrt{\text{TRAA}}$ (Myomorpha)	0.157	1.029		*	0.787	0.073	13.979	7.507	1.014	*Papagomys* sp. and *Phloeomys* sp. not included
$\sqrt{\text{TRAA}}$ (Sciuromorpha)	0.117	1.050		*	0.956	0.053	8.344	3.872	1.006	
$\sqrt{\text{TRAA}}$ (Muridae)	0.180	0.978		*	0.665	0.080	15.029	8.107	1.014	*Papagomys* sp. and *Phloeomys* sp. not included
HL	–0.610	0.995		*	0.866	0.096	18.160	7.550	1.032	
FL	–0.740	1.016		*	0.850	0.102	19.226	7.864	1.035	
PL	–0.680	0.947		*	0.850	0.100	18.526	7.596	1.035	
CL	–0.707	1.023		*	0.829	0.109	20.362	8.814	1.026	
TL	–0.659	0.951		*	0.687	0.136	24.945	10.139	1.047	
HAPDp	0.275	0.762		*	0.883	0.091	17.388	8.224	1.031	
HTDd	0.029	0.937		*	0.891	0.087	16.070	6.922	1.027	
HAPDd	0.323	0.960		*	0.903	0.086	14.509	7.915	1.022	
FAPDd	0.142	0.952		*	0.865	0.110	18.996	8.935	1.026	
FTDp	0.072	0.838		*	0.888	0.088	15.937	6.714	1.028	
TTDp	0.061	0.888		*	0.902	0.083	14.736	6.216	1.026	
TTDd	0.217	0.865		*	0.823	0.101	62.653	29.745	0.863	
TAPDp	0.084	0.955		*	0.847	0.107	74.965	31.828	0.843	
FTDd	0.009	0.935		*	0.952	0.066	13.137	5.479	1.010	Regression of femur
HAPDp/HAPDd	0.262	0.405	0.494	*	0.955	0.060	11.164	4.775	1.015	Regression of humerus
WOC/$\sqrt{\text{TRAA}}$	–0.325	0.869	0.388	*	0.967	0.043	7.998	3.900	1.005	Regression of cranium
WOC/HAPDd	–0.103	0.718	0.429	*	0.981	0.036	6.708	2.835	1.009	Regression of all skeleton

Columns represent: measurement (X_1/X_2), a (the constant), b_1 (the allometric coefficient of X_1), b_2 (the allometric coefficient of X_2), $P < 0.05$ (* when is significant), r^2 (coefficient of determination), SEE (standard error of estimate), %PE (average absolute percent prediction error), MAPE (mean absolute percent error), RE (ratio estimator) and comments. BM, body mass; WOC, width of occipital condyle; M/1AA, lower M1 area; TRAA, upper toothrow area; HL, humerus length; FL, femur length; PL, pelvis length; CL, cubit length; TL, tibia length; HAPDp, proximal humeral anteroposterior diameter; HTDd, distal humeral transversal diameter; HAPDd, distal humeral anteroposterior diameter; FAPDd, distal femoral anteroposterior diameter; FTDp, proximal femoral transversal diameter; FTDd, distal femoral transversal diameter; TTDp, proximal tibia transversal diameter; TTDd, distal tibia transversal diameter; TAPDp, proximal tibia anteroposterior diameter).

these cases we did not perform analyses by suborders or families for the same reasons we mentioned above.

Because of the results from our previous bivariate analyses, we consider that the humerus (HAPDp, HTDd, HAPDd and HL), femur (FTDd, FAPDd, FTDp and FL) and cranium (WOC, M/1AA and TRAA) are the 3 most reliable elements for predicting body masses of rodents. Therefore, we performed stepwise multiple regressions of their variables (Mendoza *et al.* 2006). In all cases the models were significant (humerus: $r^2 = 0.955$, HAPDp/HAPDd; femur: $r^2 = 0.952$, FTDd; skull: $r^2 = 0.967$, WOC/TRAA) (Table 1).

The variables included in the multiple regression of the whole skeleton were humerus, femur and cranial measurements. The stepwise method only selected 2 of them (WOC and HAPDd), creating a model with a high coefficient of determination ($r^2 = 0.981$) (Table 1).

All the regressions were accurate and precise (values of SEE, %PE and MAPE were reasonable) (Table 1). The results of the cross-validation tests were satisfactory, with high correlation between the observed and predicted scores.

Body mass estimation of *Canariomys* sp., *Hypnomys* sp. and *Muscardinus cyclopeus*

We performed estimations of the body masses of *Canariomys* sp., *Hypnomys* sp. and *M. cyclopeus* with different parameters: skull, teeth and postcranial material. Lengths of postcranial material (HL, FL, CL, PL and TL) and distal anteroposterior femoral diameter (FAPDd) were not used for estimations because of their low reliability and uncorrected validation respectively (see section 'Body mass regression models'). Similarly, the distal parameters of the humerus (HAPDd and HTDd) were removed because the shape of this articulation in rodents with digging skills differs importantly from that in other rodents (see Discussion section 'Body mass estimation of *Canariomys* sp., *Hypnomys* sp. and *Muscardinus cyclopeus*'). Results are presented in Table 2.

Data for *C. bravoi* on cranial, dental and postcranial remains were obtained from different fossil specimens (Cueva de las Palomas, Santa Cruz de Tenerife, Holocene) and from the published literature (Blanco 2005). Homogeny body mass results were obtained using simple regressions, except for the WOC parameter, which presents a lower value than the rest (WOC 901.76 g). Multiple regressions could not be performed because the literature does not offer data that associate each individual specimen/bone. The $\bar{X}$ of the species is 1571.32 g (CI 1492.5–1650.2 g). All data for *C. tamarani* were obtained from the published literature (López-Martínez & López-Jurado 1987). Data on cranial and dental material were not available for estimations. All the measurements of the postcranial yielded more or less homogenous results. The highest value was obtained analyzing TTDp (1240.60 g); TTDd yielded the lowest value (787.66 g). The body mass average of this species is 1010.65 g (CI 823.7–1197.6 g) (See all *Canariomys* results in the Fig. 2 and Table 2).

Hypnomys morpheus data were obtained from different fossil specimens (Sa Cova de Sa Bassa Blanca, Alcúdia, Holocene). Dental parameters gave similar results (√M/1AA-Sciuromorpha 158.39 g and √TRAA 161.04 g). Results from the postcranial material, however, were rather heterogeneous. The highest values were obtained assessing HAPDp (313.67 g); TAPDp yielded the lowest values (179.20 g). In this case, $\bar{\mathbf{x}}$ was 232.68 g (CI 189.7–275.7 g). In addition, *H. onicensis* data were obtained from different fossil specimens (Sa Pedrera de s'Onix, Manacor, Late Pliocene). From teeth and cranial parameters, only √M/1AA data were available to perform body mass estimations (158.33 g). The postcranial material provided more or less uniform estimations. The highest value was obtained assessing HAPDp (361.68 g); TAPDp yielded the lowest value (72.90 g). The average of all parameters is 201.47 g (CI 127.2–275.8 g). (See all *Hypnomys* results in Fig. 3 and Table 2).

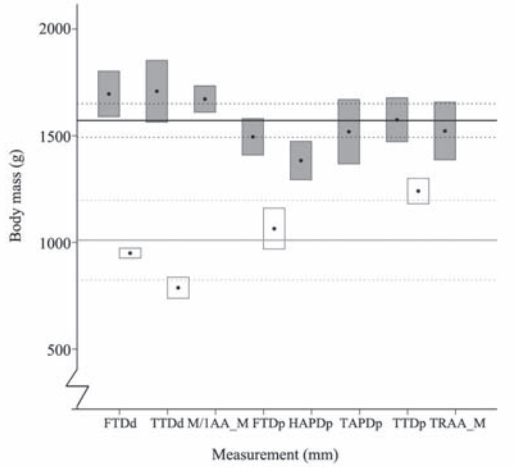

Figure 2 Body mass estimations for *Canariomys bravoi* (grey boxes) and *C. tamarani* (white boxes). *X*-axis: parameters used for body mass estimation. *Y*-axis: body mass (g). Black points: mean estimation of all specimens; box: confidence interval of the mean; horizontal lines: general average ($\bar{X}$) (black, *C. bravoi*; grey, *C. tamarani*); dotted lines: confidence interval (CI).

Table 2 Body mass estimation (in grams) of *Canariomys bravoi*, *C. tamarani*, *Hypnomys morpheus*, *H. onicensis* and *Muscardinus cyclopeus* (columns)

	Canariomys bravoi	*Canariomys tamarani*	*Hypnomys morpheus*	*Hypnomys onicensis*	*Muscardinus cyclopeus*
WOC	901.76 (736.6–1066.9)*	–	–	–	–
WOC-Muridae	675.97 (564.7–787.3)*	–	–	–	–
$\sqrt{\text{M/1AA}}$	2105.72 (2025.5–2186.0)*	–	116.15 (111.1–121.2)*	116.05 (105.9–126.2)*	170.26 (160.5–180.0)
$\sqrt{\text{M/1AA-Muridae}}$	1671.83 (1609.8–1733.8)	–	–	–	–
$\sqrt{\text{M/1AA-Sciuromorpha}}$	–	–	158.39 (151.1–165.7)	158.33 (143.6–174.9)	237.03 (227.7–251.4)*
$\sqrt{\text{TRAA}}$	1602.40 (1238.4–2087.6)*	–	161.04 (149.2–172.9)	–	–
$\sqrt{\text{TRAA-Muridae}}$	1522.24 (1386.8–1657.7)	–	–	–	–
$\sqrt{\text{TRAA-Sciuromorpha}}$	–	–	147.67 (136.7–158.6)*	–	–
HAPDp	1383.65 (1293.5–1473.8)	–	313.67 (297.4–329.9)	361.68 (325.7–397.7)	127.18 (117.2–137.2)
HTDd	–	–	–	–	140.38 (134.2–146.6)
HAPDd	–	–	–	–	41.07 (36.3–45.8)
FTDd	1695.96 (1589.5–1802.5)	949.71 (926.3–973.1)	249.94 (236.6–263.3)	186.09 (91.4–280.7)	–
FTDp	1494.75 (1409.6–1579.9)	1064.61 (968.9–1160.3)	298.05 (268.6–327.8)	285.5 (277.3–293.6)	69.95 (66.3–73.6)
TTDp	1574.93 (1472.1–1677.8)	1240.6 (1181.2–1300.0)	221.49 (156.1–286.9)	112.14 (102.6–121.7)	–
TTDd	1708.39 (1563.4–1853.4)	787.66 (738.2–837.1)	279.66 (254.8–304.5)	233.66 (224.5–242.9)	–
TAPDp	1518.84 (1367.9–1669.8)	–	179.20 (139.5–219.0)	72.90 (63.5–82.3)	–
HAPDp/HAPDd	–	–	–	–	61.35 (56.5–66.2)
$\bar{x}$	1571.32 (1492.5–1650.2)	1010.65 (823.7–1197.6)	232.68 (189.7–275.7)	201.47 (127.2–275.8)	101.70 (60.7–142.8)
$\bar{x}_G$	1567.67	996.98	225.20	178.66	90.12
W_M	2532.30	1569.36	367.07	345.82	100.55

Left column: parameter used to estimate the average body mass of each species, confidence interval in brackets. The last 3 rows represent the average of the species: arithmetic mean ($\bar{x}$), geometric mean ($\bar{x}_G$) and the weighted mean (W_M). The values marked with a star were not included in the averages (see text). BM, body mass; WOC, width of occipital condyle; M/1AA, lower M1 area; TRAA, upper toothrow area; HL, humerus length; FL, femur length; PL, pelvis length; CL, cubit length; TL, tibia length; HAPDp, proximal humeral anteroposterior diameter; HTDd, distal humeral transversal diameter; HAPDd, distal humeral anteroposterior diameter; FAPDd, distal femoral anteroposterior diameter; FTDp, proximal femoral transversal diameter; FTDd, distal femoral transversal diameter; TTDp, proximal tibia transversal diameter; TTDd, distal tibia transversal diameter; TAPDp, proximal tibia anteroposterior diameter).

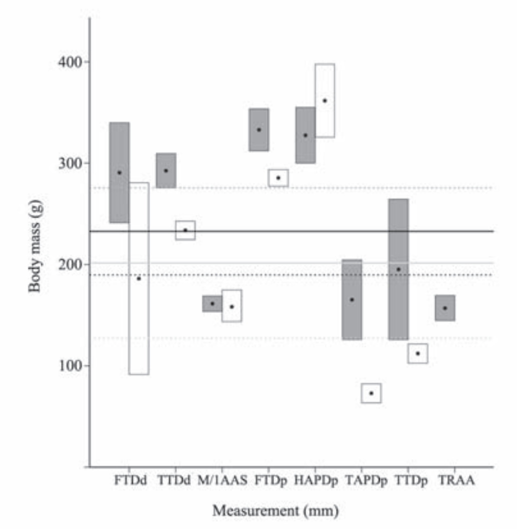

Figure 3 Body mass estimations for *Hypnomys morpheus* (grey boxes) and *H. onicensis* (white boxes). *X*-axis: parameters used for body mass estimation, *Y*-axis: body mass (g). Black points: mean estimation of all specimens; box: confidence interval of the mean; horizontal lines: general average ($\bar{X}$) (black, *H. morpheus*; grey, *H. onicensis*); dotted lines: confidence interval (CI).

Cranial, dental and postcranial data on *M. cyclopeus* were obtained from different fossil specimens (Punta Nati-3, Ciutadella de Menorca, Pliocene). The scarce material yielded variable results. The highest value was obtained assessing $\sqrt{M/1AA}$ (170.26 g); HAPDd provided the lowest values (41.07 g). $\bar{\mathbf{X}}$ is 101.70 g (CI 60.7–142.8 g) (See all the results in the Table 2).

DISCUSSION

Body mass regression models

Historically, dental parameters (molars) are the elements most frequently used for predicting body mass in rodents, because of their high presence in the fossil record and their easy determination (Legendre 1986; Damuth & MacFadden 1990; Janis 1990; MacFadden & Hulbert 1990; van Valkenburgh 1990; Parra & Jaeger 1998; Schwartz *et al.* 1995; Hopkins 2008). Cranial measurements are also frequently used to perform body mass estimations (Millien 2008; Rinderknecht & Blanco 2008; Bover *et al.* 2010). Although a size increase of the animal is associated with an increase in the size of teeth and skull, these skeletal structures are not involved in weight bearing. Therefore, their evolution also depends on other selective pressures that may trigger changes in their size (Fortelius 1990; Janis 1990). It is widely recognized that postcranial skeletal elements best reflect the support of the animal's weight (Legendre & Roth 1988; Damuth & MacFadden 1990; Jungers 1990; Scott 1990; Biknevicius *et al.* 1993; Egi 2001; Mendoza *et al.* 2006; Millien & Bovy 2010). The limbs (stylopods and zeugopods) support the weight of the animal. Zeugopods (ulna, radius, tibia and fibula) are modified by the locomotor specializations and preferences of the animal. Therefore, forelimb (humerus) and hindlimb (femur) stylopods are preferable for the estimation of body mass (Damuth & MacFadden 1990; Scott 1990). The robustness of stylopodium is much more indicative of the animal's body mass than is its length (Damuth & MacFadden 1990; Scott 1990; van Valkenburgh 1990; Christiansen 1999; Egi 2001) because the force for supporting the body mass is proportional to the area of the transversal section (Currey 2006). Cranial and dental parameters do not to provide estimates as reliable as those of postcranial parameters (Legendre & Roth 1988; Damuth 1990; Janis 1990; Scott 1990; van Valkenburgh 1990; Egi 2001; Reynolds 2002). Bearing this in mind, we performed different models according to the nature of the source (cranial, dental, postcranial length, postcranial articulations and multiple). The results are excellent in all the cases, but some nuances can be observed.

The differences between the simple regression models performed with cranial, dental and articular postcranial material are minimal, and all of them present results close to coefficient of determination of 0.9 or higher, and low %PE. In contrast, the values of bone length are less satisfactory (lower r^2 and greater %PE). Thus, the use of these variables for predicting the body mass is less recommendable (Damuth & MacFadden 1990; Scott 1990; van Valkenburgh 1990; Christiansen 1999; Egi 2001), but they may be helpful in supplementing other estimations. Furthermore, the lengths of the postcranial elements are highly variable because of their distinctive use in richochetal, gliding, fossorial and semifossorial locomotions that characterize the various rodent taxa (Samuels & van Valkenburgh 2008). It is also important to emphasize the results from tibial (zeugopodial) parameters. Although the variability explained by the model is good, the percentage prediction errors (%PE) of 2 of its measures are high (TTDd and TAPDp) (Damuth & MacFadden 1990; Scott 1990). Therefore, it is important to interpret their results cautiously and to additionally include other estimations.

Spectacular results are obtained from the width of the occipital condyle (WOC), a measurement never used before to estimate body mass in micromammals. Although their results are excellent both from simple and multiple regression models, this measurement could only be applied in 1 species (*C. bravoi*) (see Results section 'Body mass estimation of *Canariomys* sp., *Hypnomys* sp. and *Muscardinus cyclopeus'*). The fragility of the bone and the process of fossilization are important factors in the preservation of the fossils. Where preserved, however, the condyles are excellent proxies of body mass.

Results from multiple regressions are more satisfactory than those from simple regression. Nevertheless, the fossil remains are seldom in association or anatomical position, hampering the utilization of multiple regressions and forcing the use of simple regression. Bivariate analyses, however, are constrained by phylogenetic legacy and ecological adaptations, while multiple analyses compensate those by using several measures without redundant information (using the stepwise method only the informative variables are entered into the model) (Mendoza *et al.* 2006).

We performed cranial and dental estimation models both on a highly heterogeneous group (all species) and on more homogeneous groups (suborder and family level). It must be emphasized that the values obtained from the Sciuromorpha suborder are much better than the 'all rodents' values in the 3 cases (Hopkins 2008). This, however, does not happen in all the groups. This is the case of Myomorpha suborder and Muridae family, which present models with lower coefficient of determination and greater %PE, especially in the TRAA measurement. These differences between groups of similar taxonomic level (suborder) might result from the higher degree of heterogeneity in Myomorpha and Muridae (with large number of species, over 700, and high variability in locomotion, habitat and diet). The dentition is highly specialized at a clade level (Morgan *et al.* 1995; Hopkins 2008) and, therefore, it is preferable to use both equations (heterogeneous and a more homogeneous ones) and compare the results with the postcranial data.

Body mass estimation of *Canariomys* sp., *Hypnomys* sp. and *Muscardinus cyclopeus*

Two of the species present skills for digging, associated to a semifossorial mode of life (López-Martínez & López-Jurado 1987; Bover *et al.* 2010; Michaux *et al.* 2012). Consequently, some of their traits not only represent the size (body mass), but they are also associated to the use (Reynolds 2002). Fossorial and semifossorial rodents have short forelimbs with larger muscle attachments (with increased deltopectoral crest of the humerus, larger epicondyles of the humerus and oleocraneon process of the ulna) (Samuels & van Valkenburgh 2008). They show a high humeral epicondylar index (HEB = HTDd/HL functional). When this index is performed with *C. bravoi* data, a high value is obtained (0.338). This confirms the modification of the distal humerus (HTDd and HAPDd) as a consequence of their semifossorial specialization (use) and it is preferable not to use these measurements to estimate their weight as they overestimate the real mass. The locomotion of *M. cyclopeus* has not yet been studied, but our results suggest that they follow the same tendency observed in *Canariomys* sp. and *Hypnomys* sp. (great values of HTDd and low of HAPDd). Although it seems plausible that this species presented some skills for digging as well, we could not exclude the results of the distal humerus because of the poor sample and because we do not know with confidence that *M. cyclopeus* had a fossorial lifestyle.

The 2 species of *Canariomys* present a large body mass, as expected from their large cranial and postcranial bones. *C. bravoi* weights approximately 1.5 kg and *C. tamarani* approximately 1 kg. These results are in accordance with some previous studies (López-Martínez & López-Jurado 1987), but not with others that predicted a larger (Michaux *et al.* 1996) or a lower body mass (Michaux *et al.* 2012). The weight of *C. tamarani* is estimated only based on postcranial material and the results are more or less homogeneous. In contrast, *C. bravoi* presents body mass estimations around the average, except for the WOC parameter, which predicts a lower body mass and is considered a parameter that needs more research to understand its low values in this species. Therefore, it was removed when the averages were calculated (Fig. 2, Table 2). Among the estimations performed with M/1AA and TRAA, we chose Muridae instead of 'all rodents'. The former is in better agreement with the postcranial material, while the latter clearly overestimates body mass.

The 2 anagenetic species of *Hypnomys* had considerable body masses. *H. onicensis* weighted approximately 200 g, while *H. morpheus* had a mass of 230 g. The 2 species inhabited the same island in different temporal periods, thus indicating a continuous increase in body mass during the evolution of the *Hypnomys* sp. lineage. Our estimations are in agreement with the results of other authors (Bover *et al.* 2010). For both species, the results of M/1AA-Sciuromorpha data are preferable, although they lie below the average. Surprising are the values obtained from HAPDp and TAPDp, especially in the *H. onicensis* case, which are far from the average line. The scarce remains may contribute to these rare values, and future studies will show whether this is due to the poor sample or whether these measurements are true outliers (related with locomotion instead of body mass). It is interesting to observe that for all parameters *H. morpheus* is larger than *H. onicensis*, except for HAPDp, a parameter that will need to be assessed in depth. Although the 2 species present different average values, the confident intervals overlap. It is logical in view of the 2 species assessed as anagenetic; one is the precursor of the other.

Muscardinus cyclopeus is the Miocenic glirid from Minorca (Bover *et al.* 2008). Because of its limited area and the bad preservation of the fossil record, *M. cyclopeus* material is very scarce (Agusti *et al.* 1982). Thus, the sample used to perform the analysis is small. Our estimations are rather heterogeneous. In contrast to the above results, the M/1AA estimation based on 'all rodents' equations (170 g) is preferable over the more specific ones (Sciuromorpha order) (237 g) as it better fits the postcranial results (around 100 g).

Island rule

The body masses of these insular giants lie well above those of their living relatives (Fig. 4a–c). Sundry hypotheses have been formulated to explain the phenomenon of insular gigantism; most of them associate this tendency with the specific ecological parameters of the islands, such as low predation or competition (Lomolino *et al.* 2012). According to Palkovacs (2003), the body size differences in island mammals are the results of adaptive changes in age and size at maturity (life history traits) and depend primarily on the relative importance of the extrinsic mortality rate and resource availability. For small mammals, decreased extrinsic mortality triggers delayed maturity and reproduction at a larger size. These individuals will have higher fitness than those that follow the mainland strategy under high predation risk of maturing early and reproducing small. Although the absence of extrinsic mortality is the main factor that affects the biology of the island rodents (small mammals) and its body size, resource availability can have a secondary effect, limiting their maximum body mass. Because of their bounded area, the carrying capacity of islands is limited and permits a finite number of primary producers only. The biology of first consumers (herbivores) is affected by the total number of primary producers (energetic resources) and, consequently, by the dimensions of the island. Therefore, the observed differences in body mass between small mammals that live in similar ecosystem structures (coexistence of few mammals and absence of top predators) are not related to the low extrinsic mortality but, instead to the availability of resources. The differential effect of predation and resources is a likely explanation in the case of *Canariomys* (Fig. 4a). The 2 species inhabited different islands with very similar ecosystems. The rats coexisted with lizards and birds; hence, interspecific competition was low (Rando 2003). The only predation pressure came from birds of prey, especially from *Buteo bu-*

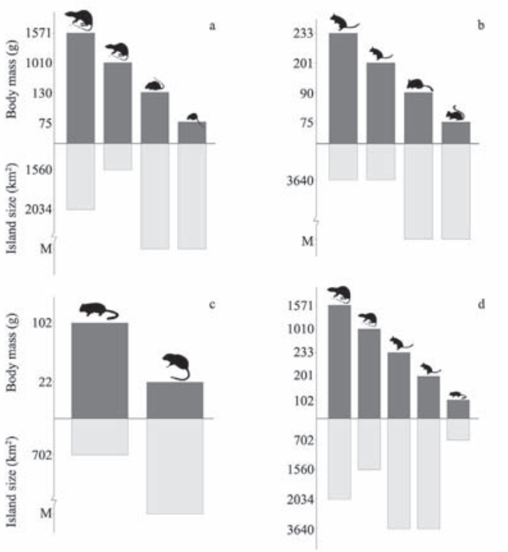

Figure 4 Body masses of extinct rodents (†) and their extant mainland relatives (∞), and areas of their respective island (or mainland). The upper dark boxes represent body mass (estimation for fossil taxa and values from the published literature [Silva & Downing 1995] for extant rodents). The lower light boxes represent the island size (the area of the island; M: mainland). a, Diagram for *Canariomys* sp., from left to right: *C. bravoi* (†), *C. tamarani* (†), *Pelomys fallax* (∞) and *Arvicanthis niloticus* (∞). b, Diagram for *Hypnomys* sp., from left to right: *H. morpheus* (†), *H. onicensis* (†), *Eliomys quercinus* (∞) and *E. melanurus* (∞). c, Diagram for *Muscardinus cyclopeus*, from left to right: *Muscardinus cyclopeus* (†) and *M. avellanarius* (∞). d, Diagram for insular extinct rodents, from left to right: *C. bravoi* (†), *C. tamarani* (†), *H. morpheus* (†), *H. onicensis* (†) and *M. cyclopeus* (†). In all cases the island areas represent their current extension. The sea level might have changed slightly as a consequence of the glacial and interglacial periods. In the Canary Islands, these variations are not very steep (Zazo *et al.* 1993). The same pattern can be observed in the Gymnesic Islands, with the exception of the connection between Majorca and Minorca at the Plio–Pleistocene limit (Bover *et al.* 2008). The studied populations of *Hypnomys* sp. are not from this period.

teo Linnaeus, 1758 (the only potential depredators with a great range of dispersion) (Sánchez Marco 2010). As suggested by the remains of *Canariomys*, however, it seems that they only fed on them occasionally. The 2 species increased their body mass as a consequence of the low extrinsic mortality (neither competition nor depredation), but *C. bravoi* attained a larger size than *C. tamarani*. The former lived on a larger island than the latter (Fig. 4a), which had lower resource levels.

The *Hypnomys* sp. case is quite different. The 2 species (*H. onicensis* and *H. morpheus*) differ in body mass although they inhabited the same island area (Fig. 4b). However, we are talking 2 anagenetic species. The older continued to evolve towards a new species with a larger body mass, thus confirming that *H. onicensis* had not yet achieved in keeping with the island size and productivity. Although *Hypnomys* sp. dwelled on a larger island than *Canariomys* sp., *Canariomys* is bigger in size (Fig. 4d). Both genera inhabited simple ecosystems but with noticeable differences. Thus, *Canariomys* sp. neither had predators nor competitors. *Hypnomys*, instead, inhabited an area highly populated by birds of prey (e.g. *Aquila chrysaetos* Linnaeus, 1758, *Aquila dalberti* Brehm, 1861 and *Haliaeetus albicilla* Linnaeus, 1758), one of them specialized on it (*Tyto balearica* Mourer-Chauvire, Alcover, Moya & Pons, 1980) (Arnau *et al.* 2000). This is confirmed by the presence of rodent remains in avian pellets (Adrover 1972). Moreover, *Hypnomys* shared the island with other mammals (a small-to-medium-sized goat, *Myotragus* sp.; and a small shrew, *Nesiotites* sp.) (Alcover *et al*. 1981). Although they were not direct competitors, their coexistence may have prevented *Hypnomys* from exploring new ecological niches, which was not the case for *Canariomys*. In the case of *Hypnomys* sp., body mass resulted from a compromise between low extrinsic mortality (only a few birds of prey) and resource availability; in the case of *Canariomys*, the body size was a consequence of the total absence of predators (neither mammalian predators nor birds of prey, leading to an important decrease in extrinsic mortality) and the resource supply. Thus, apart from the different phylogenetic constraints of both genera, these important differences in the ecological assemblage (predators) largely explain the differences in body size.

Muscardinus cyclopeus was compared with its living relative (Fig. 4c). *M. cyclopeus* is the smallest of the 5 species studied. This is not surprising because it lived on the island with the smallest land area (Fig. 4d). Predation and resources level (area island) most likely determined its body mass. More detailed studies will be needed to reach further conclusions.

To sum up, our analysis yielded different equations to estimate the body masses of mainland and island fossil rodents. All the parameters used provided considerable results, except for the length of long bones, DTW and PTD, which should not be used alone and should be interpreted with caution. The equations for dental (M1AA and TRAA) and postcranial material do not show important differences in their results. For M1AA, however, results from the equations performed with more closely related species (suborder or family level) were more in accordance with those from the postcranial material. Multiple regressions were overall more satisfactory, but their use is very limited because complete fossils are scarce. The estimated body masses of *C. bravoi* (1.5 kg), *C. tamarani* (1 kg), *H. morpheus* (230 g), *H. onicencis* (200 g) and *M. cyclopeus* (100 g) allow inferences regarding the ecological conditions that trigger the island rule. *Canariomys* sp. inhabited an island free of predators and competitors; here, hence, the island area (resource availability) is the key factor that permitted *C. bravoi* (Tenerife) to grow larger than *C. tamarani* (Gran Canaria). *Hypnomys* sp. evolved on the same island in an anagenetic lineage from a small sized (*H. onicensis*) to a larger form (*H. morpheus*) during the Pleistocene–Holocene period. Although the Gymnesic rodents inhabited a larger island than *Canariomys*, the latter species was much larger. Contrary to *Canariomys*, *Hypnomys* was subject to higher predation pressure (*Tyto balearica*, among others). Therefore, we suggest that extrinsic mortality was a major selection pressure for this insular dormouse, checking a further size increase (apart from possible constraints due to different phylogenetic backgrounds). Further studies are needed to understanding the role of resource availability (island area/productivity) under absence of predation (*Canariomys* case).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Table S1 Extant species included in the study, insularity, average body mass of the species and bibliography of body mass

Figure S1 Graphics of the pairwise regression models (log-log scale) between a skeletal parameter (*x*-axis) and body mass (*y*-axis). The parameters used are the following: (A) width of the occipital condyle (WOC) using all species; (B) WOC–Hystricomorpha; (C) WOC–Myomorpha; (D) WOC–Sciuromorpha; (E) WOC–Muridae; (F) lower first molar area (M/1AA) using all species; (G) M/1AA–Hystricomorpha; (H) M/1AA–Myomorpha; (I) M/1AA–Sciuromorpha; (J) M/1AA–Muridae; (K) lower toothrow area (TRAA) using all species; (L) TRAA–Hystricomorpha; (M) TRAA–Myomorpha; (N) TRAA–Sciuromorpha; (O) TRAA–Muridae; (P) humerus length (HL); (Q) femur length (FL); (R) pelvis length (PL); (S) cubit length (CL); (T) tibia length (TL); (U) proximal humeral anteroposterior diameter (HAPDp); (V) distal humeral transversal diameter (HTDd); (W) distal humeral anteroposterior diameter (HAPDd); (X) distal femoral transversal diameter (FTDd); (Y) distal femoral anteroposterior diameter (FAPDd); (Z) proximal femoral transversal diameter (FTDp); (AA) proximal tibia transversal diameter (TTDp); (AB) distal tibia transversal diameter (TTDd); and (AC) proximal tibia anteroposterior diameter (TAPDp).

SUPPLEMENTARY INFORMATION

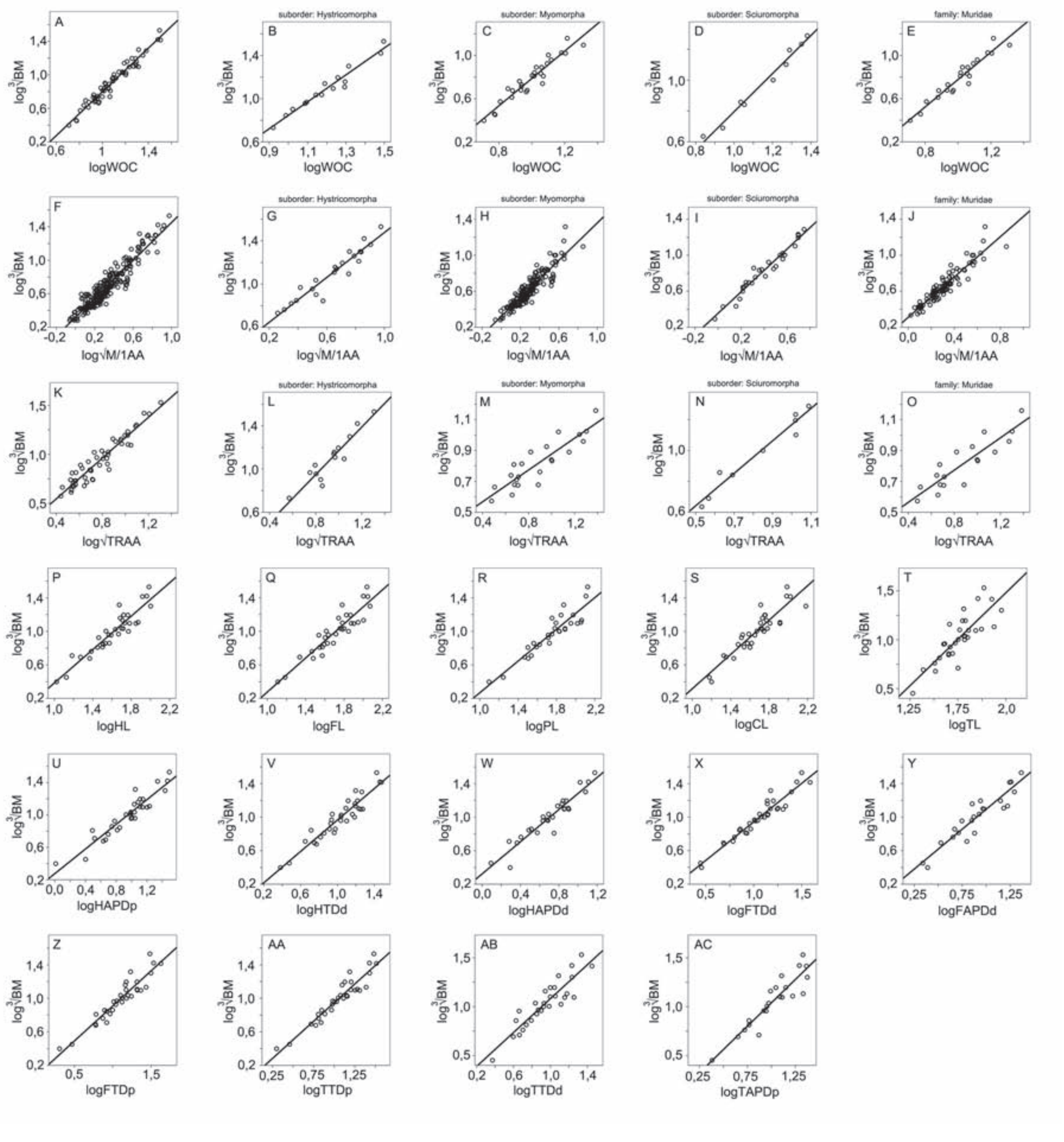
Table S1 Extant species included in the study (columns: species, family, n=number of individuals (WOC/√M1AA/√TRAA/postcranial), insularity (¶ when data from insular and continental specimens are mixed), average body mass of the species, bibliography of body mass.

SPECIES	FAMILY	N	INSULARITY	BODY MASS (grams)	BIBLIOGRAPHY
Aethomys hindei	Muridae	14/14/14/0		68.679	RMNH Collection
Apodemus sylvaticus	Muridae	20/0/0/0		23.55	UB Collection
Arvicanthis niloticus	Muridae	18/18/18/0		105.833	UIB Collection
Arvicola amphibus	Cricetidae	19/0/0/19		119.895	UB Collection
Arvicola sapidus	Cricetidae	5/5/5/5		192.4	MNCNM Collection
Bandicota indica	Muridae	10/10/10/0	Taiwan	468.2	RMNH Collection
Bathyergus suillus	Bathyergidae	9/9/9/8		733.6	Silva and Downing (1995)
Capromys pilorides	Capromyidae	1/1/1/0	Cuba	2630	De Magalhaes and Costa (2009)
Campromys pilorides pilorides	Capromyidae	1/1/1/1	Cuba	1920	Silva and Downing (1995)
Castor fiber	Castoridae	6/4/4/6		17633	Silva and Downing (1995)
Cavia aperea	Caviidae	2/1/1/1		341	Silva and Downing (1995)
Cavia porcellus	Caviidae	9/9/9/0	Taiwan	509.8	RMNH Collection
Cricetomys gambianus	Muridae	10/10/10/0		1156.250	RMNH Collection
Cricetus cricetus	Cricetidae	19/18/19/7		276.4	Silva and Downing (1995)
Crossomys moncktoni	Muridae	1/1/1/0	New Guinea	165	Silva and Downing (1995)
Dasyprocta leporina	Dasyproctidae	7/7/7/5		2108.33	Silva and Downing (1995)
Dasyprocta leporina leporina	Dasyproctidae	11/11/11/0		2950	Bicknevicius et al. (2003)

Dolichotis patagonum	Caviidae	6/3/3/3		8000	Silva and Downing (1995)
Echiothrix leucura	Muridae	6/5/5/0	Indonesia	267.29	Musser (1990)
Eliomys quercinus	Gliridae	68/57/56/11	¶	80.683	UIB and UB Collection
Geomys breviceps	Geomyidae	4/4/4/0		138.8	English (1932)
Geomys pinetis cumberlandius	Geomyidae	1/1/1/0		171.5	Castleberry and Laerm (2007)
Geomys pinetis floridanus	Geomyidae	5/5/5/0		165	Sendzimir (2008)
Glis glis	Gliridae	9/9/9/0		117.778	UIB Collection
Gymnuromys roberti	Nesomyidae	1/1/1/0	Madagascar	97.5	Smith et al (2003)
Heliophobius argenteoeinereus	Bathyergidae	13/13/13/0		156.25	RMNH Collection
Hydrochaeris hydrochaeris	Caviidae	2/2/2/2		39125	Silva and Downing (1995)
Hydromys chrysogaster	Muridae	8/8/8/4	New Guinea	596.125	Silva and Downing (1995)
Hypogeomys antimena	Nesomyidae	2/2/2/2	Madagascar	1185	Silva and Downing (1995)
Hystrix cristata	Hystricidae	4/4/4/3		18334	Silva and Downing (1995)
Jaculus orientalis	Dipodidae	11/10/10/5		135.2	Silva and Downing (1995)
Kerodon rupestris	Caviidae	1/1/1/1		800	Silva and Downing (1995)
Lemniscomys barbarus	Muridae	3/3/3/0		52.333	RMNH Collection
Leopoldamys sabanus	Muridae	3/3/3/0	Java	315.43	Silva and Downing (1995)
Lophiomys imhausi	Muridae	1/1/1/1		755	Ernest (2003)
Marmota bobak	Sciuridae	1/1/1/0		7300	Animal Diversity Web
Marmota himalayana	Sciuridae	1/1/1/0		5000	Smith et al. (2003)
Marmota marmota	Sciuridae	11/11/11/2		2010	Silva and Downing (1995)

Marmota monax	Sciuridae	11/11/11/2		3844	Silva and Downing (1995)
Mus musculus	Muridae	18/0/0/16		15.619	UB Collection
Myodes glareolus	Cricetidae	12/0/0/12		22.604	UB Collection
Myoprocta acouchy	Dasyproctidae	11/11/11/2		1280	Silva and Downing (1995)
Ondatra zibethicus	Cricetidae	14/14/14/14		1026.39	Silva and Downing (1995)
Papagomys armandvillei	Muridae	3/2/2/1	Indonesia	8890	Paleobiology Database
Pedetes capensis	Pedetidae	7/6/6/2		2500	RMNH Collection
Phloeomys cumingi	Muridae	1/1/1/1	Philippines	1946.33	Smith et al. (2003)
Pithecheir melanurus	Muridae	9/9/9/1	Java	108	Silva and Downing (1995)
Plagiodontia aedium	Capromyidae	1/0/0/1	Santo Domingo	1267	De Magalhaes and Costa (2009)
Rattus argentiventer	Muridae	20/20/20/0	Java	154.375	UB Collection
Rattus norvegicus	Muridae	12/0/0/12		266.833	UB Collection
Rattus rattus	Muridae	34/33/33/0	¶	108.176	UB and UIB Collection
Ratufa bicolour	Sciuridae	11/11/11/2	Java	1000	Silva and Downing (1995)
Rhizomys sumatrensis	Spalacidae	12/10/10/4		3000	Silva and Downing (1995)
Sciurus granatensis	Sciuridae	3/3/3/3	Trinidad Tobago	374	Ernest (2003)
Sciurus vulgaris	Sciuridae	20/20/20/1		334.86	Silva and Downing (1995)
Spalax micropthalamus	Muridae	2/2/2/0		470	Smith et al. (2003)
Sundamys mulleri	Muridae	10/9/9/0	Sumatra	332.75	Silva and Downing (1995)
Thryonomys swinderianus	Thryomyidae	4/4/4/2		3860	Silva and Downing (1995)

Figure S1 Graphics of the pairwise regression models (log-log scale) between a skeletal parameter (*x*-axis) and body mass (y-axis). The parameters used are the following: (A) width of the occipital condyle (WOC) using all species; (B) WOC-Hystricomorpha; (C) WOC-Myomorpha; (D) WOC-Sciuromorpha; (E) WOC-Muridae; (F) lower first molar area (M/1AA) using all species; (G) M/1AA-Hystricomorpha; (H) M/1AA-Myomorpha; (I) M/1AA-Sciuromorpha; (J) M/1AA-Muridae; (K) lower toothrow area (TRAA) using all species; (L) TRAA-Hystricomorpha; (M) TRAA-Myomorpha; (N) TRAA-Sciuromorpha; (O) TRAA-Muridae; (P) humerus length (HL); (Q) femur length (FL); (R) pelvis length (PL); (S) cubit length (CL); (T) tibia length (TL); (U) proximal humeral anteroposterior diameter (HAPDp); (V) distal humeral transversal diameter (HTDd); (W) distal humeral anteroposterior diameter (HAPDd); (X) distal femoral transversal diameter (FTDd); (Y) distal femoral anteroposterior diameter (FAPDd); (Z) proximal femoral transversal diameter (FTDp); (AA) proximal tibia transversal diameter (TTDp); (AB) distal tibia transversal diameter (TTDd); and (AC) proximal tibia anteroposterior diameter (TAPDp).



Chapter 5

The Island Rule and the native island of *Mikrotia magna* (Muridae, Rodentia) from Terre Rosse deposits (Gargano, Apulia, Italy): inferences from its body mass estimation

Moncunill-Solé B, Jordana X, Köhler M

Historical Biology (to be submitted)

THE ISLAND RULE AND THE NATIVE ISLAND OF *MIKROTIA MAGNA* (MURIDAE, RODENTIA) FROM TERRE ROSSE DEPOSITS (GARGANO, APULIA, ITALY): INFERENCES FROM ITS BODY MASS ESTIMATIONS

Historical Biology (to be submitted)

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Abstract

Terre Rosse deposits (Late Miocene; Gargano, Italy) are distinguished by the presence of a complex of fossil remains with insular traits, where *Mikrotia* genus stands out among them. Several biological studies have been conducted in this genus, but its body mass has not yet been calculated accurately. Our aim is to reconstruct its weight, a paramount aspect of organismal biology, especially on islands (Island Rule) where mammals modify its size (giants or dwarfs). Our analysis predicted weights ranging from 1300 g to 1900 g (old and young populations respectively). These values are similar to those of *Canariomys bravoi*, a murid species that dwelled in an oceanic island (without competitors and with only very few predators). The presence of a large number of micromammals on the Gargano paleo-island suggests a high interspecific competition (*Mikrotia* had direct competitors such as *Prolagus* or cricetids), which may conduct to only moderate gigantism or even dwarfism of small mammals. Thus, the enormous weight of *M. magna* is striking and unexpected taking into consideration the selective pressures (high interspecific competition) of Gargano. One of the most plausible explanations for the huge body mass of *M. magna* is its arrival from another island of the paleo-archipelago, which has also been suggested by several stratigraphic and taxonomic studies. A native island with lower number of competitors might be the principal explanation for such degree of gigantism.

Keywords: Archipelago effect – Gigantism – Interspecific competition – Island Rule – *Mikrotia* – Palkovacs' model – Resources limitation

Introduction

When Freudenthal (1971) described the rich bulk of micromammals found in Terre Rosse deposits (Late Miocene; Gargano, Apulia, Italy) by its “gigantism and aberrant morphologies”, he principally referred to a new genus of murid with a “rapid and amazing evolution”. Not long after, it was Freudenthal (1976) himself, who erected the new genus *Mikrotia* (Rodentia, Muridae) for these exceptional remains (*nomen novum* for *Microtia*, see Freudenthal 2006). *Mikrotia* is the most widespread and characteristic mammal of the Terre Rosse. For this reason, it gave name to the faunistic complex recovered there (*Mikrotia* assemblage). For the moment, at least five different lineages of *Mikrotia* are identified, some of which cohabited during the same time period (phase 3 of Terre Rosse) (Masini et al. 2010: Fig. 4; Maul et al. 2014: Fig. 4). However, three species are only described formally: *Mikrotia parva* (Freudenthal 1976) (found only in the oldest fissures), *Mikrotia maiuscola* (Freudenthal 1976) (the “resident” lineage) and *Mikrotia magna* (Freudenthal 1976) (the largest species that is only found on the youngest fissures) (Freudenthal 1976, 2006; Masini et al. 2013: Fig. 6). The disharmonic biota recovered from Terre Rosse (overrepresentation of some taxa and underrepresentation of other, relative to mainland source) and their endemic modifications (including *Mikrotia*) were identified as traits of an insular population (Freudenthal 1971; Masini et al. 2010). Accordingly, during Late Miocene, Terre Rosse deposits were part of a wider system of isolated land areas (palaeo-archipelago that included also the Scontrone and Palena-Capo di Fiume sites) termed as Abruzzo-Apulian palaeobioprovince (De Giuli et al. 1986a, 1986b, 1987; Abbazzi et al. 1996; Rook et al. 2006; Mazza and Rustioni 2008). In this respect, the faunal assemblage found in Terre Rosse deposits (Gargano paleo-island) is considered a relic of a very long history of endemisation (Butler 1980; Abbazzi et al. 1996; Rook et al. 1999, 2000; Masini et al. 2008). The biota comprises a large representation of terrestrial endemic micromammals and birds, including rodents [e.g. *Hattomys* sp. Freudenthal 1985, *Mikrotia* sp. (Freudenthal 1976), *Stertomys* sp. Daams and Freudenthal 1985], pikas (*Prolagus apricenicus* Mazza 1987 and *Prolagus imperialis* Mazza 1987), gymnures (*Apulogalerix pusillus* Masini and Fanfani 2013) and birds of prey (e.g. *Tyto gigantea* Ballmann 1973, among others), although non-endemic species were also recovered [e.g. *Dryomys apulus* Freudenthal and Martín-Suárez 2006 or *Lartetium* cf. *dehmi* (Viret and Zapfe 1952)]. Conversely, macromammals were scarcer and are represented by endemic gymnures (*Deinogalerix* Freudenthal 1972), ruminants (*Hoplitomeryx* Leinders 1984) and otters (*Paralutra garganensis* Willemsen 1983, with sparse finds) (for more details see Masini et al. 2010: Tab. 1). The last phase of Terre Rosse is characterized by a drop of biodiversity, possibly as a result of a reduction of the island area (Masini et al. 2008). Unfortunately, as a consequence of the Early Pliocene flooding, the whole faunal assemblage got extinct. In the Early Pleistocene, the area emerged again, but this time connected to the mainland. This allowed non-insular species to colonize these habitats.

The ecosystems of islands are characterized by the presence of dwarf and giant mammals, following the trend of insular endemic species to converge in body size (BS) termed as Island Rule (IR) (Foster 1964; Van Valen 1973). Although several hypotheses have been proposed in order to explain this ecogeographical rule (see Foster 1964; Van Valen 1973; Heaney 1978; Lomolino 1985; Schwaner and Sarre 1988; among others), nowadays it is a controversial issue (Lomolino et al. 2013 and references therein). The body mass (BM, proxy of BS) is a paramount trait in the life of any organism because it shows high correlation with morphological, physiological, behavioral, metabolic, ecological and life-history variables (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Kardong 2007). For this reason, insular populations of mammals are also distinguished by differences in their demography, life history, behavior and morphology (Island Syndrome, IS; Adler and Levins 1994). Adler and Levins (1994) described that extant insular populations of rodents show higher survival rates (longer longevity), higher and more stable densities, reduced reproductive outputs and differences in behavior with regard to mainland relatives. Studies of insular extant and extinct lagomorphs have reported modifications of the morphology of skeleton (low sacropelvic angle or stiff vertebral column), indicating low gear locomotion (Yamada and Cervantes 2005; Quintana et al. 2011). Up to now, the few biological studies of the small mammals of the Terre Rosse deposits are focused on the genus *Mikrotia*. It is characterized by a notable increase of BS [Millien and Jaeger (2001) estimated a BM of 400.2 g for M. magna] and an increase of the hypsodonty and complexity of the molars (development of additional lamellae) (Freudenthal 1976; Masini et al. 2010). The morphology and microstructure of its teeth pointed out that this genus used the incisors for digging and that its diet was abrasive and herbivorous (rhizomes and roots, and probably grasses) (Zafonte and Masini 1992; Parra et al. 1999). Kolb et al. (2015) carried out paleohistological descriptions of the femora of several specimens of *M. magna*. The thin sections of this species displays: in the middle part of the cortex parallel-fibred bone with mainly reticular vascularisation and strong remodeling (secondary osteons), and in the inner and outer parts lamellar bone with mainly radial vascularisation. This composition of bone tissue is similar to the one observed in extant murid rodents (Kolb et al. 2015). These authors observed four to five lines of arrested growth (LAGs) in one individual (RGM.792085) and the high amount of remodeling bone is interpreted as a consequence of the high individual ages. They suggested that this species has a similar bone histology and life history (LH) than their mainland relatives. On the other hand, the evaluation of the paleohistology of *M. magna* done by Moncunill-Solé et al. (2013) discerned 15 LAGs in the external fundamental system (EFS) and they suggested this value to be minimum longevity of the species that may indicate a slow LH.

Because of the aforesaid correlations between BM and LH traits, the precision of accurate reconstruction of BM shifts of insular extinct species is absolutely indispensable. Firstly, it delves into the biology and ecology of extinct species, which allows a better understanding of the species; and secondly it allows a more accurate approach to the IR. The greatest obstacle that we find when working in paleontology is that BM cannot be measured directly from individuals. However, the allometry (between BM and skeletal traits) and statistical procedures allow us to carry out precise BM estimations (Damuth and MacFadden 1990; Moncunill-Solé et al. 2014). The distinctive insular features (especially for its striking size) and abundance of *M. magna*, in addition to the complexity of faunal assemblage of Terre Rosse (large presence of micromammals), make this species an interesting group. Our interest is in the reconstruction of BM of several populations of this species recovered at different fissures of Terre Rosse using regression models and, in last instance, delving into the BM trends observed on islands (IR).

Abbreviations

BM – Body mass
BS – Body size
F8 – Cava Fina F8 fissure filling
F9 – Cava Fina F9 fissure filling
FAPDd – distal femoral antero-posterior diameter
FTDd – Distal femoral transversal diameter
FTDp – Proximal femoral transversal diameter
HAPDd – Distal humerus antero-posterior diameter
HAPDp – Proximal humerus antero-posterior diameter

HTDd – Distal humerus transversal diameter
IR – Island Rule
IS – Island Syndrome
LH – Life History
LHT – Life History Theory
SG – San Giovannino fissure filling
UNIFI – Università degli Studi di Firenze

Materials and methods

We studied postcranial material of *M. magna* from the fissures Cava Fina F8, Cava Fina F9 and San Giovannino (coded as F8, F9 and SG respectively; Table 1). These fissures are the most important ones in providing remains of *M. magna*, in addition to P1B (De Giuli et al. 1987; Masini et al. 2010: Fig. 4; Masini et al. 2013: Fig. 6). The studied remains belong to the collection of the 1980s field work led by the late Claudio De Giuli and are stored in the Scienze della Terra department of the Università degli Studi di Firenze (UNIFI, Italy). Postcranial material of *M. magna* was identified from the set of rodent species for its distinctly larger dimensions, as other authors done previously (Parra et al. 1999, Kolb et al. 2015, among others). We did not assume BM differences between sexes in extinct murids because sexual dimorphism of extant small mammals is considered minimal (Lu et al. 2014). The postcranial bones with fused epiphyses were considered suitable for carrying out the BM estimation study, and those with unfused or broken epiphyses were excluded. Stylopods (humeri and femora) are preferable for weight reconstructions because they are less modified by the mode of locomotion (specializations) and habitat preferences of individuals (Damuth and MacFadden 1990; Scott 1990). Moreover, teeth (incisors and molars) of the genus *Mikrotia* are so modified that their use as BM proxies is not appropriate (Freudenthal 1976; Parra et al. 1999). Hence, we decided to use femora and humeri for estimating the BM of *M. magna*. The bad preservation of the remains (principally fragmented) prevented the use of length for reconstructing the BM. However, Moncunill-Solé et al. (2014) pointed out that the antero-posterior and transversal diameters of the epiphysis of stylopods are good BM estimators in rodents ($r^2 > 0.85$). The following measurements (described in Moncunill-Solé et al. 2014; modified from Cabrera 1980) were taken with a digital caliper (0.05 mm error): proximal femoral transversal diameter (FTDp), distal femoral antero-posterior diameter (FAPDd), distal femoral transversal diameter (FTDd), proximal humerus antero-posterior diameter (HAPDp), distal humerus transversal diameter (HTDd) and distal humerus antero-posterior diameter (HAPDd). We estimated the BM of the species applying the allometric models described in Moncunill-Solé et al. (2014).

	POSTCRANIAL MATERIAL	
FISSURE FILLING	FEMUR	HUMERUS
F8	13	26
F9	3	36
SG	2	2

Columns: fissure filling (F8, F9 or SG sorted biochronologically) and postcranial element (femur or humerus).

Table 1. Postcranial material of *M. magna* used for the study. See the abbreviation section for the codification of fissure fillings.

Results

The BM estimations of *M. magna* of the different fissures are shown in Table 2. As a result of the large fragmentation of postcranial bones and the lack of fusion of some epiphyses, as well as the different abundances of individuals in the fissures, a different number of individuals were studied in each of the fissures and for each measurement (Table 2). In this respect, the fissures F8 and F9 are those which contain the largest sample, while SG remains are only represented by 4 elements (2 femora and 2 humeri) (Table 2). The BM estimations of *M. magna* from F8 have been performed with four parameters: FAPDd, FTDd, HTDd and HAPDd, with a notable higher representation of distal humeri (26 elements). The estimated BMs are quite different (FAPDd, 1886 g; FTDd, 1366 g; HTDd, 1602 g; and HAPDd, 935 g). A similar pattern can be observed in the F9 fissure, where only 3 femora were measured compared to a large number of humeri. In F9, the BMs predictions are also variable (FAPDd, 1555 g; FTDd, 1254 g; HTDd, 1638 g; HAPDd, 931 g; and HAPDp, 1314 g). In the case of SG, the sample is scarcer and the values quite heterogeneous (from 1313 g for HAPDd to 2421 g for HTDd). As a result of the differences of sample sizes, we decided to calculate weighted means instead of the common arithmetic one (Table 2). Additionally, we also calculated averages with the database split by skeletal element (femora and humeri) (Table 2).

Following the biochronological order of the fissures, F8 and F9 belong to the phase 3a while SG is younger (phase 3c) (Freudenthal 1976; de Giuli et al. 1987; Masini et al. 2010: Fig. 4). For this reason, when the BM estimations were compared between fissures, the results of F8 and F9 (older fissures) are more in agreement between them than with SG, where the values seems to be higher (Table 2, Fig. 1). However, these differences are not statistically significant (Kruskal Wallis, $p > 0.05$), probably due to the low sample size of SG and the heterogeneity of BM predictions. Consequently, our results do not support a BS increase of *M. magna* throughout its evolution in Terre Rosse statistically, although the mean of SG is greater than that of the other two fissures fillings.

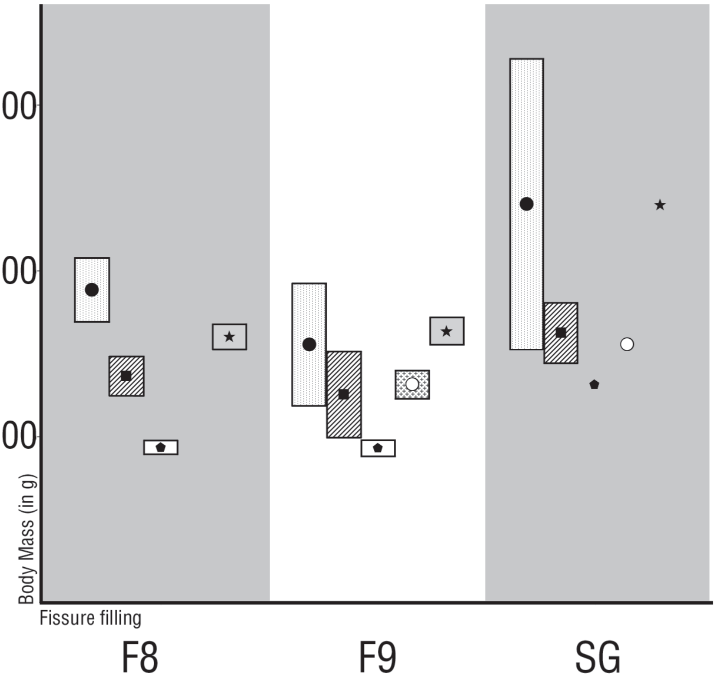

Figure 1. Boxplots (mean and confidence interval) of BM estimations of *M. magna* by fissure filling. The measurements are the following: FAPDd (pattern of dots and black dot), FTDd (pattern of stripes and black square), HAPDd (white pattern and black pentagon), HAPDp (pattern of crosses and white dot) and HTDd (grey pattern and black star). The values are presented in Table 2. See the abbreviation section for the codification of fissure fillings and measurements.

Table 2. BM estimations (in grams) of *M. magna*. The grey rows are the mean of the species by fissure filling: 1) using all postcranial bones (MEAN), 2) using femoral measurements (MEAN-Femur) and 3) using humeral measurements (MEAN-Humerus). See the abbreviation section for the codification of fissure fillings and measurements.

FISSURE FILLING	MEASUREMENT	N	BM MEAN	CI_L	CI_U
F8	FAPDd	9	1885.576	1691.800	2079.353
F8	FTDd	13	1366.171	1247.490	1484.860
F8	HTDd	21	1601.580	1526.183	1676.976
F8	HAPDd	26	935.318	893.166	977.470
F8	MEAN	69	1343.22	-	-
F8	MEAN-Femur	22	1578.65	-	-
F8	MEAN-Humerus	47	1233.01	-	-
F9	FAPDd	3	1555.374	1186.658	1924.090
F9	FTDd	3	1254.150	994.242	1514.058
F9	HTDd	26	1637.911	1555.484	1720.338
F9	HAPDd	34	931.218	881.951	980.485
F9	HAPDp	2	1314.076	1228.947	1399.205
F9	MEAN	68	1254.47	-	-
F9	MEAN-Femur	6	1404.76	-	-
F9	MEAN-Humerus	62	1239.92	-	-
SG	FAPDd	2	2403.814	1528.570	3279.060
SG	FTDd	2	1627.261	1445.260	1809.261
SG	HTDd	1	2420.854	-	-
SG	HAPDd	1	1312.728	-	-
SG	HAPDp	1	1564.861	-	-
SG	MEAN	7	1908.66	-	-
SG	MEAN-Femur	4	2015.54	-	-
SG	MEAN-Humerus	3	1766.15	-	-

Columns: fissure filling (F8, F9 or SG sorted biochronologically), measurement (FAPDd, FTDd, HAPDd, HTDd, HAPDp), sample size (N), body mass mean (BM Mean, in grams) and the confidence interval (CI_L, lower confidence interval; and CI_U, upper confidence interval).

Discussion

The BM of Mikrotia magna

Our research study is the first to estimate the BM of *M. magna* using postcranial bones (femora and humeri). *Mikrotia magna* has always been considered a giant rat, and the large BMs obtained in our analyses confirm the distinctive and huge BS of this extinct species (noticeable in SG) (Table 2). However, our BM predictions are in marked contrast to estimations done previously (400.2 g, from SG), which used the antero-posterior diameter of the lower incisor as proxy (Millien and Jaeger 2001). The BM predictions of *M. magna* based on teeth parameters (molars or incisors) are likely less accurate than ours for several reasons. Firstly, teeth are considered worse proxies of BM than postcranial bones. Generally, the correlation between BS and tooth size is always lower than that observed between BS and postcranial dimensions (Fortelius 1990; Janis 1990), because skeletal elements are related to weight bearing (Damuth and MacFadden 1990; Scott 1990; Biknevicius et al. 1993; Mendoza et al. 2006; Millien and Bovy 2010). Secondly, *Mikrotia* genus is characterized by highly modified molars (with the addition of transversal crests in M_1 and M^3, and very hypsodonts) (Freudenthal 1976), which are not comparable to the general patterns of extant rodents. Finally, Parra et al. (1999) noticed that *M. magna* probably used its skull and incisors for excavating the soil (tooth-digger) and, thus, its dimensions and shape are likely modified accordingly. For all these reasons, we believe that our predictions based on postcranial elements provide more accurate and suitable estimations and, hence, they better evidence the true BM of this extinct murid.

It is, however, also true that some bones can provide inaccurate estimations of BM (e.g. consequence of its peculiar locomotion). In the case of fossil insular rodents, it should be taken into account that these in general show fossorial skills for searching fallback (alternative) resources when the food is scarce. For example, this is observed in *Hypnomys* sp. Bate 1918 (Gymnesic Islands, Spain) and *Canariomys* sp. Crusafont and Petter 1964 (Canary Islands, Spain). On the one hand, *Hypnomys morpheus* Bate 1918 was described with greater fossorial postcranial adaptations that its mainland relative (Bover et al. 2010; Quintana Cardona and Moncunill-Solé 2014) and it shows a robust mandible adapted to a more abrasive diet (Hautier et al. 2009). On the other hand, *Canariomys bravoi* Crusafont and Petter 1964 had some skills for digging and scratching the soil (Michaux et al. 2012). Generally, the fossorial and semifossorial postcranial adaptations of rodents are principally related with the forelimbs: distal epiphysis of the humerus, oleacraneon process of the ulna and phalanges and claws of the manus. These species are described by an enlargement of the muscle attachments of the deltopectoral crest and of the epicondyles of the humerus (Samuels and Van Valkenburgh 2008). As stated earlier, Parra et al. (1999) observed some teeth and skull characters of *Mikrotia* that are indicative of digging activities and an abrasive diet. They described *M. magna* as a tooth-digger and stated that postcranial skeleton (humeri and femora) is little specialized for this lifestyle (Parra et al. 1999). Therefore, postcranial measurement should not overestimate the BM of this species.

On the other hand, the large number of distal humeri (noticeable in F8 and F9) is striking when compared with the number of other epiphyses (Table 1 and 2). This is essentially due to the fact that other epiphyses are mainly unfused (B. Moncunill-Solé, pers. observ.). Generally, the secondary centers of ossification (epiphyses) of mammals fuse to the diaphysis at skeletal maturity, moment when longitudinal growth ceases. However, in rodents (rats, mice and others) there are certain growth plates that remain open into old age (Dawson 1925; Mehta et al. 2002). Thus, while distal humerus (capitulum and trochlea) fuses when sexual maturity is attained, the growth plates of the femur fuse later in ontogeny (Nilsson et al. 2002). Although the potential longitudinal growth of femora is kept, the growth is restricted later after certain time (Roach et al. 2003). We calculated two BM means of *M. magna* by postcranial element (femora and humeri) (Table 2) in order to observe potential trends that remain hidden. The differences between these two BM means (femora and humeri) are not statistically significant (T-test, $p > 0.05$) (Table 2). Thus, the large number of distal humeri should not cause bias problems in the *M. magna* estimations.

Therefore, we decided to take into consideration both skeletal elements (femora and humeri) for the calculation of BM mean of *M. magna*. We estimate that in F8 and F9 *M. magna* weighed around 1300 g (from a minimum of 881.951 g to a maximum of 2079.353 g), and in the case of SG, its weight was around 1908.66 g (from a minimum of 1312.728 to a maximum of 3279.06 g). Some authors noticed an increase in BS of this species throughout its evolution (using incisors as BM proxies, element related with its fossorial lifestyle) (Millien and Jaeger 2001; Van der Geer et al. 2013), but in our case study the BS increase is not demonstrated statistically ($p < 0.05$). Probably, the low number of postcranial elements in SG is the main reason for these non-significant results, but no more measureable humeri and femora were recovered. SG is the fissure filling just before the beginning of phase 4 of Gargano paleo-island (Masini et al. 2010: Fig. 4), where a drastic drop in diversity of small mammals is observed (extinction of several species) possibly linked to a reduction of island area (De Giuli et al. 1987, 1990; Masini et al. 2008). Therefore, the small sample size of distal humeri in SG (in comparison with the previous F8 and F9) can be interpreted as an initial decrease in the abundance of this species prior to its extinction. Our observation is in agreement with the low frequencies of *M. magna* molars recovered in this fissure (De Giuli et al. 1987). On the other hand, we cannot discard that problems of sedimentation/taphonomy (bad preservation) or the gathering and washing of less sediment material from this fissure filling could be the main reasons of this low number of specimens.

The Island Rule and the native island of **M. magna**

Insular ecosystems are characterized by specific selective pressures. Firstly, islands are described by their geographical limitations and, hence, by their low resource quantity. Due to these factors, the biodiversity of islands is reduced, and, generally, their ecosystems are disharmonic (unbalanced) and impoverished, triggering a lower interspecific competition (MacArthur and Wilson 1967). Besides, their secondary consumers consist basically of reptiles and birds of prey (with some exception, e.g. Sardinia and Sicily) (Sondaar 1977; Van der Geer et al. 2010), indicating a lower predation pressure than in mainland habitats. Community ecologists have proposed several hypotheses taking into consideration these insular selective regimes to explain the modification of BS of their endemics (predation hypothesis, food availability hypothesis or social-sexual hypothesis) (see Foster 1964; Van Valen 1973; Heaney 1978; Lomolino 1985; Schwaner and Sarre 1988; among others). On the other hand, the shift of BS on islands can be interpreted as a result of changes in the LH of individuals in these new environments. Based on r/K selection theory and Life History Theory (LHT), Palkovacs (2003) proposed a theoretical predicting taking into account the extent to which low extrinsic mortality and limitation of resources of islands affect the LH of endemic fauna. The direction of the BM shift (towards larger or smaller BS) relies on the balance of these two pressures (Palkovacs 2003: Fig. 1). Generally, small mammals are considered to be most affected by lower extrinsic mortality (modification of reaction norm) and to a lesser degree by resource limitation (minimal modification of growth rate, see empirical evidences in Orlandi-Oliveras et al. 2016). Following LHT (Stearns 1992), a lower mortality rate entails an increase in the age at maturity and a large BS (giant morphotype). In some cases, however, resource limitation could be predominant over lower extrinsic mortality in small mammals (e.g. rodents strictly specialized in their diet). When this happens, insular species develop a dwarf morphotype (e.g. *Perognathus* sp. Wied-Neuwied 1839 from Central American Islands) (Lawlor 1982; Brown et al. 1993; Durst and Roth 2015). According to the theoretical model proposed by Palkovacs (2003), the reductions of BS of small mammals would be related to a drop in the growth rate (as in the case of large mammals), but this is not confirmed by empirical studies. On the other hand, the degree of the BS shift (if the change is more or less sharp with respect to the mainland ancestor) is particular of each island and depends on island traits: area, degree and type of isolation, number of competitors and predators, among others traits (Lomolino et al. 2012 and references therein). Moncunill-Solé et al. (2014), studying extinct species of rodents, pointed out that the amount of resources (island area) may play an important role in determining the maximum BS of the giants (small mammals) in special cases where the predators are almost absent (*Canariomys* case study) (see also McNab 2002, 2010). Lomolino et al. (2013) suggested that the most extreme cases of gigantism and dwarfism are observed in the fossil record probably as a consequence of the long period of ecological isolation, in contrast to the extant fauna. Nevertheless, as Sondaar pointed out (1987, 1991), extreme modifications (BS or morphological traits) are not found in extant endemic faunas because of their susceptibility to human activities (considered a super-predator). We have modified the natural ecosystems by introduction of exotic species (competitors and predators) and infectious diseases, alteration of the habitats (agricultural activities, deforestation), and extermination of endemics (hunt) (Masseti 2009). In other words, we have destroyed the natural ecosystems of islands and their native faunas, by altering their selective regimes.

The Terre Rosse deposits (Gargano paleo-island) were characterized by the presence of only crocodiles, snakes and birds of prey as predators and by a high diversity of rodents and other micromammals (insectivores and lagomorphs) (Masini et al. 2010: Tab. 1). Although we do not know specifically the diet of each of the micromammal species, it is likely that some of them belonged to the same ecological guild (especially the congeneric species, e.g. species of *Mikrotia* genus). This interspecific competition in Terre Rosse is appreciable with the extinctions of certain genera of micromammals that are only present in the first stages documented (e.g. *D. apulus* or *L.* cf. *dehmi*), or of those that tried to join to this faunal complex in several geological times (unsuccessful immigrations) (De Giuli and Torre 1984, Masini et al. 2010, 2013). Following the theoretical model of Palkovacs (2003), we would expect for this set of small mammals with an important interspecific competition a moderate BS increase (when the lower extrinsic mortality predominates in front of resources limitation) (Angerbjorn 1985; Herczeg et al. 2009) or even dwarf morphotypes (when the resource limitation predominates over low extrinsic mortality) (Lawlor 1982; White and Searle 2007). In accordance with this, in the fauna of Terre Rosse we noticed the presence of several species with smaller BS than their mainland relatives (possible dwarfs): *A. pusillus* (that is smaller than their Miocene representatives), the lineage of *Stertomys daamsi* Freudenthal and Martín-Suárez 2006 – *Stertomys degiulii* Rinaldi and Masini 2009 (that reduced its BS throughout its evolution), and *M. parva* (that shows a slight BS decrease) (De Giuli and Torre 1984; De Giuli et al. 1987; Masini et al. 2010, 2013). In addition, *Apodemus* sp. Kaup 1829 inhabited all fissure fillings of Terre Rosse, but without showing any endemic morphological trait besides a slight increase of BM only in the youngest fissures (De Giuli et al. 1987; Masini et al. 2010, 2013). These dwarf species contradict the expected pattern of IR for small mammals proposed by Foster (1964) and Van Valen (1973).

In the particular case of *Mikrotia*, De Giuli et al. (1987) pointed out that the most important competitors of this genus were the pikas (*Prolagus* Pomel 1853) because both groups are forms specialized in grazing (open environments, grasslands) (De Giuli and Torre 1984). Taking into account the studies of Zafonte and Masini (1992) and Parra et al. (1999), *Mikrotia* genus could also compete with cricetids (*Hattomys*), known for their burrow skills and omnivore diet (that includes roots, tubers, stems, earthworms, etc.) (Nowak, 1999; Poor 2005). Moreover, the several species of *Mikrotia* that coexisted in the same period also probable competed with each other (De Giuli et al. 1986a, Masini et al. 2013: Fig. 6). In light of the above, we suggest an important interspecific competition and, hence, strong resource limitation for this genus. As stated above, following the model of Palkovacs (2003), this high interspecific competition prevented that this genus could achieve very large morphotypes. Hence, the BM of *M. magna* (1.3-1.9 kg) estimated in our research is striking and unexpected. Its weight is comparable to that of *C. bravoi* (BM=1.5 kg), the extinct Canarian murid that did not have competitors or predators on its island (Moncunill-Solé et al. 2014). The intense competition with *Prolagus* (grasses), cricetids (roots and rhizomes) and other *Mikrotia* species for resources would most likely have prevented such impressive increase in BM.

One of the most probable explanations for the large BS of *M. magna* is that it came from another native island (another ecosystem) of the paleo-archipelago. Our biological/ecological observation is in agreement with stratigraphic and taxonomic studies, where it is emphasized the sudden apparition of *M. magna* specimens in the fossil deposits of Terre Rosse during the phase 3 (Freudenthal 1976; De Giuli et al. 1986a). *Mikrotia magna* does not seem to have a previous evolutionary lineage in Gargano paleo-island (Freudenthal 1976; De Giuli et al. 1986a; Masini et al. 2010: Fig. 3) and its arrival may be consequence of the "archipelago effect" (De Giuli et al. 1986a; Abbazzi et al. 1996). In other words, their entrance in Terre Rosse is assumed to occur "jumping" from a neighboring island of the paleo-archipelago (De Giuli and Torre 1984; De Giuli et al. 1986b; Masini et al. 2008, 2010; Maul et al. 2014). From this point of view, two biological/ecological facts may explain the enormous BS of *M. magna*:

1) Firstly, *M. magna* could be the descendent of a large mainland species (ancestor) different to the ancestor of the other lineages of *Mikrotia* found on Terre Rosse. However, Masini et al. (2013) suggested that the Murinae nov. gen., nov. sp. found on the new discovered fissure filling (M013) of Terre Rosse represents the ancestor of *Mikrotia*. Probably all the species derived from a unique common ancestor, and then it diversified on different islands of the paleo-archipealgo.

2) Secondly, the native island of *M. magna* have different selective regimes that have enabled this BS shift (De Giuli and Torre 1984). It is important to notice here that stratigraphic and taxonomic studies of the other largest species of micromammals (*Stertomys laticrestatus* Daams and Freudenthal 1985 and *Prolagus imperialis*) found in Terre Rosse deposits also arrived from neighboring islands (Masini et al. 2010: Fig. 4) and they did not evolve in the high competitive environment of Gargano paleo-island. According to the model proposed by Palkovacs (2003), small mammals increase their BM when they experience lower extrinsic mortality than in the mainland habitats, and when resource limitation imposed by the geography of island (area, productivity, and competitors) does not limit growth. Possibly, a low number of direct competitors in the native island in contrast to Gargano, and, hence, a less restricted resource limitation may be the most important factor to explain it.

When *M. magna* arrived to the Gargano paleo-island (phase 3), it was able to join to a new insular ecosystem full of rodents (high competition), very integrated, co-evolved and endemic (De Giuli and Torre 1984; Masini et al. 2008). Previously, other *Mikrotia* lineages from neighboring islands also tried to settle there, but they did not obtain satisfactory results and became extinct (*M. parva* or *Mikrotia* sp. b) (De Giuli and Torre 1984; Masini et al. 2013; Maul et al. 2014). Two reasons can explain the satisfactory establishment of *M. manga* to Gargano paleo-island:

1) Following F1 fissure, previously to the *M. magna* entrance, an environmental change took place to a drying out habitat (De Giuli et al., 1987). This new resource environment supposed more resources and, hence, an advantage to grassland dwellers (*Mikrotia* and *Prolagus* species).

2) The arrival of *M. magna* was associated to the extinction (surely by competitive exclusion) of the endemic lineage of cricetids (*Hattomys*) (Masini et al. 2010, 2013). This fact also supposed an increase of resource availability for *Mikrotia* genus.

Confidently, these two not mutually exclusive reasons allowed *M. magna* to establish satisfactorily in the ecosystems of the Gargano paleo-island, in contrast to the previous unsuccessful immigrations of other species of *Mikrotia*.

The posterior reduction of the island area as a result of the external geodynamic forces caused a trophic crisis in the equilibrate biota, and resources became more limited (De Giuli et al. 1987; Masini et al. 2008). As a consequence, *M. magna* went extinct at this point (phase 3c), together with *S. laticrestatus* and *M. maiuscola*. It is around the time of their extinction (fissure F32, decrease of interspecific competition) when the species that had tended to produce dwarf morphotypes (lineage *S. daamsi – S. degiulii*, *A. pusillus* and *Apodemus* sp.) showed a slightly increase in its BS (De Giuli et al. 1987).

Conclusions

Mikrotia magna weighed around 1300 g (from 881.95 to 2079.35 g) in F8 and F9 and around 1908.7 g (from 1312.73 to 3279.1 g) in SG, although the increase between the assessed fissure fillings is not statistically significant. These values are in strong contrast to previous estimations based on teeth as BM proxies. These latter parameters are less well correlated with BM and, hence, our postcranial estimations are more reliable. The overrepresentation of distal humeri in our sample does not represent a bias problem, because it is the result of differences in the fusion of growth plates. The important presence of micromammals in Gargano suggests a high interspecific competition and a severe limitation of resource for the species. This fact is noticeable by the disappearance of several not endemic genera and the exclusion of newcomers that arrive to the island in several geological times. According to Palkovacs' model, it is suggested that Gargano's micromammals can achieve moderate gigantism or even dwarf morfotypes, because although they have a lower extrinsic mortality than the mainland, the resource limitation is very important. This reduction in BS (dwarf morphotype) is observed in *A. pullisus*, *M. parva* and *S. daamsi – S. degiulii*, which contradict the expected pattern of IR. The BM values obtained in our research for *M. magna* are stricking for a micromammal living in this fauna complex, taking into account that it had direct competitors for resources: congeneric species (*M. maiuscola*), *Prolagus* (grasses) and cricetids (roots, tubercles). These biological/ecological remarks suggest that *M. magna* cannot achieve this large BS in Gargano and another native island, with a less number of competitors, has been proposed. Our result is in agreement with stratigraphic and taxonomic studies, which evidenced that *M. magna* did not have a previous evolutionary lineage in Gargano and had a sudden appearance in the fossil register. Its entrance to Gargano supposed the extinction of the cricetid lineage and coincided with a climatic change that favored grassland dwellers. Our hypothesis that the high interspecific competition in small mammals of Gargano (entailing a resource limitation) prevented that these species achieved a very large BS is reinforced by the fact that the largest species of other micromammals also arrived from other islands of the paleo-archipelago.

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Chapter 6

The weight of fossil leporids and ochotonids: body mass estimation models for the order Lagomorpha

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The weight of fossil leporids and ochotonids: body mass estimation models for the order Lagomorpha

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Keywords
Lagomorpha; body mass; allometric models; *Prolagus*; *Nuralagus rex*; fossil; extinct; ancestor species.

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Abstract

Lagomorphs are widespread around the world, but little is known about the biology and ecology of their fossil ancestors. In this case, knowing the body mass of these extinct species is of principal interest because it is correlated with physiological, morphological and life history attributes. Moreover, insular fossil rabbits, hares and pikas, which became spectacular giants with huge weights and dramatic shifts in their life histories, encourage curiosity in the research world. Our principal aim is to create allometric models between skeletal parameters and body weights with extant species of the order Lagomorpha (both ochotonids and leporids). These regressions can then be applied to the fossil register to estimate the body mass of the extinct lagomorphs. The models are satisfactory in all cases, although weaker relationships were obtained when we analyzed dental parameters. Multiple models have slightly better results than bivariate ones, but their use is limited to complete bones or skeletons. These body mass estimation models were tested in three different fossil lagomorphs: *Prolagus apricenicus*, *Prolagus* cf. *calpensis* and *Nuralagus rex*. In all three cases, the results from dental variables were discarded due to the fact that these species may not follow the allometric relationship between teeth and body mass of standard lagomorphs. Other variables, such as the proximal anteroposterior diameter of the humerus in *N. rex*, were also removed for their implications in fossorial lifestyle. We ultimately estimated a weight of around 600 g for *P. apricenicus*, 300 g for *P.* cf. *calpensis* and 8000 g for *N. rex*. Differences in extrinsic mortality explain the important differences in body masses between the two *Prolagus* species. The results of *N. rex* cannot be compared with the giant *Prolagus* due to phylogenetic differences.

Introduction

The order Lagomorpha, which originated in the early Paleocene-Eocene in Asia (Asher *et al*., 2005; Ge *et al*., 2013), is now widespread all over the world, occupying a broad spectrum of habitats. Morphological differences (dental formula, maxillar and nasal bones, among other traits) as well as behavior and locomotion make it possible to distinguish between the two lagomorph families: Leporidae (rabbits and hares) and Ochotonidae (pikas) (López-Martínez, 1989). Leporids originated 55 million years ago and show adaptations for quick movements with long hindlegs for running or bounding (Chapman & Flux, 2008). The diversification of this family started in the Late Miocene, coinciding with a period of global cool and dry conditions (Ge *et al*., 2013). Some of these genera endure today (*Lepus* Linnaeus, 1758 and *Oryctolagus* Lilljeborg, 1873), while others went extinct (*Alilepus* Dice, 1931; *Hypolagus* Dice, 1917; *Notolagus* Wilson, 1937; *Pratilepus* Hibbard, 1939; and others). On the other hand, *Ochotona* Link, 1795 is the only extant genus of pikas, principally restricted to Asia. Ochotonids originated at least as early as the Eocene (50 mya) (Chapman & Flux, 2008) and underwent an important radiation during the Miocene (*Eurolagus* López-Martínez, 1977; *Gymnesicolagus* Mein & Adrover, 1982; *Prolagus* Pomel, 1853; *Titanomys* von Meyer, 1843; and others) (Ge *et al*., 2013). The family Ochotonidae spread from Asia to Europe before the leporids, arriving at the Iberian Peninsula in the Early Miocene. The family Leporidae arrived in the Late Miocene, concurrent with profound faunistic modification within the European ochotonids: *Lagopsis*, *Eurolagus* and some endemic species of *Prolagus* became extinct (López-Martínez, 1989).

The body masses (BMs) of mammals are correlated with many physiological, morphological and life history attributes: home range, ecological interactions, behavioral adaptations, locomotion, brain size, resource requirements, basal metabolic rate, demography and life history traits (growth rate, life span and age at sexual maturity, among others) (Calder, 1984; Damuth & MacFadden, 1990; Brown, Marquet & Taper, 1993; Raia, Barbera & Conte, 2003; Lomolino, 2005; Köhler, 2010; Jordana & Köhler, 2011; Marín-Moratalla, Jordana & Köhler, 2013). BM within Lagomorpha ranges greatly from pikas with the smallest weights (70–250 g) to rabbits and hares the highest (0.5–4 kg and 1–5 kg, respectively) (Silva & Downing, 1995). Their intermediate BM position between small and large herbivores makes them suitable for sustaining populations of small- and medium-sized (foxes, birds of prey, and others), or even large-sized (wolves or bears) predators (Valverde, 1964). Fossil lagomorphs endemic to islands (Masini *et al.*, 2008; Yamada & Sugimura, 2008) are an intriguing case, presenting shifts in BM (Lomolino, 2005; Angelone, 2007; Quintana, Köhler & Moyà-Solà, 2011) following the island rule (Foster, 1964; Van Valen, 1973), as a consequence of the different insular ecosystem pressures (Palkovacs, 2003). Insular mammals not only present shifts in BM but also in their life histories (Raia *et al.*, 2003; Köhler, 2009; Jordana *et al.*, 2012). In the light of all this, knowing the BMs of extinct mammal species is of principal interest for understanding their biology and ecology. The allometric relationship between BM and bone measurements for extant species allows the development of BM regression models for reconstructing the average weight of extinct species (Damuth & MacFadden, 1990). The absence of models for estimating the BMs of the order Lagomorpha (Quintana Cardona, 2005 and Quintana *et al.*, 2011 only provided models for leporids) limits our understanding of its fossil species. By expanding the database of Quintana Cardona (2005) with new leporid and ochotonid species, we aim to construct allometric models between BM and postcranial, cranial and dental parameters. We will apply our models to three extinct species of lagomorphs: *Prolagus* sp. (*Prolagus apricenicus* Mazza, 1987 and *Prolagus* cf. *calpensis* Major, 1905), the most important extinct ochotonid genus of the European Cenozoic (López-Martínez, 1989); and *Nuralagus rex* (Quintana *et al.*, 2011), a giant insular leporid with a unique set of derived features, such as adaptations to a low-gear palmigrade/plantigrade quadrupedalism and a reduction in brain size (Quintana *et al.*, 2011).

Materials and methods

Taxonomy used in the current paper follows Wilson & Reeder (2005).

Species database

Data for extant species of lagomorphs were collected from 48 species, 12 belonging to Ochotonidae and 36 to Leporidae (Supporting Information Table S1), maximizing the taxonomic diversity and minimizing the effects of phylogeny (Mendoza, Janis & Palmqvist, 2006). The body size range covers the entire diversity of Lagomorpha, from small pikas to large leporids, making it appropriate for BM estimation on fossil records. The collections come from the Smithsonian Institution National Museum of Natural History with complementary data from Quintana Cardona (2005).

The fossil material consists of the lagomorph species *Prolagus* sp. and *N. rex* (Table 1). Two species of *Prolagus* were studied: *P. apricenicus* from Cava Fina F8, Gargano (Upper Miocene, Gargano, Italy) is stored in Università di Firenze, Italy; and *P.* cf. *calpensis* from Casablanca I (Late Pliocene, Almenara, Spain) is housed in Institut Català de Paleontologia Miquel Crusafont, Spain. The data of *N. rex* (Pliocene, Minorca, Spain) are taken from Quintana Cardona (2005).

Measurements

Measurements of length and anteroposterior and transversal diameters of the long bone (femora, humerus and tibia) epiphyses were taken following the criteria of Quintana Cardona (2005) (Fig. 1). Measurements of skull and teeth are: width of occipital condyles (WOC), total length of lower premolars and molars, and maximal width and length of the lower M1 (Fig. 1) (Quintana Cardona, 2005). Abbreviations are described in Table 2. Generally, BMs were gathered from the literature (Silva & Downing, 1995; see more references in Supporting Information Table S1). A digital electronic precision caliper (0.05 mm error) was used.

Statistical models

The model used to estimate the BMs of extinct animals was allometric (Damuth & MacFadden, 1990), expressed as a power function $Y = aX^b$. The power function was log transformed, obtaining a linear relationship ($\log Y = \log a + b \log X$) (Quinn & Keough, 2002). The data were fitted by the method of least squares (OLS, Model I) using stepwise methodology for multiple models (Quinn & Keough, 2002). The homogeneity of variances was controlled through residual plots (predicted Y vs. residuals) and outliers with Cook's distance (D_i). Species with $D_i > 1$ were eliminated and the model was reconstructed again. The precision and adjustment of the allometric models were evaluated by: the coefficient of determination, r^2; the standard error of the estimate, SEE (= √residual mean square); the average absolute per cent prediction, %PE (= [(observed-predicted)/predicted]*100); and the mean absolute per cent prediction error, $\mathrm{MAPE}\left(=\frac{100}{n}\sum_{t=1}^{n}\left|(y_t-\hat{y}_t)/y_t\right|\right)$ (Smith, 1980, 1984). Cross-validations were undertaken to test the suitability of

Table 1 Fossil material used for the body mass estimation

	Sample					
Species	*N*	M/1	TRL	F	H	T
Prolagus apricenicus	42	18	0	24	0	0
Prolagus cf. *calpensis*	133	27	2	5	87	12
Nuralagus rex	113	0	20	32	34	27

Columns: *N*, total sample size; M/1, number of first lower molars; TRL, number of lower toothrow length; F, number of femora; H, number of humerus; T, number of tibia.

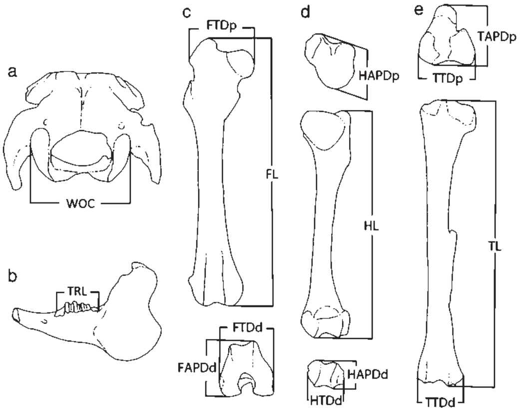

Figure 1 Measurements of the cranium and postcranial bones. (a) Cranium. WOC (width of occipital condyles); (b) Mandible. TRL (lower toothrow length); (c) Femora. FL (femur length), FTDp (proximal femoral transversal diameter), FTDd (distal femoral transversal diameter), FAPDd (distal femoral anteroposterior diameter); (d) Humerus. HL (humerus length), HAPDp (proximal humeral anteroposterior diameter), HTDd (distal humeral transversal diameter), HAPDd (distal humeral anteroposterior diameter); (e) Tibia. TL (tibia length), TTDp (proximal tibia transversal diameter), TAPDp (proximal tibia anteroposterior diameter), TTDd (distal tibia transversal diameter).

Table 2 Abbreviations of the measurements taken from the material

Bone	Measurement	Abbreviation	Figure
Teeth	Width of the first lower molar (M/1)	WM/1	–
Teeth	Length of the first lower molar (M/1)	LM/1	–
Teeth	Area of the first lower molar (M/1)	M/1AA	–
Teeth	Toothrow length	TRL	1b
Teeth	Toothrow area	TRAA	–
Skull	Width of occipital condyles	WOC	1a
Femur	Femur length	FL	1c
Femur	Proximal femoral transversal diameter	FTDp	1c
Femur	Distal femoral anteroposterior diameter	FAPDd	1c
Femur	Distal femoral transversal diameter	FTDd	1c
Humerus	Humerus length	HL	1d
Humerus	Proximal humeral anteroposterior diameter	HAPDp	1d
Humerus	Distal humeral anteroposterior diameter	HAPDd	1d
Humerus	Distal humeral transversal diameter	HTDd	1d
Tibia	Tibia length	TL	1e
Tibia	Proximal tibia anteroposterior diameter	TAPDp	1e
Tibia	Proximal tibia transversal diameter	TTDp	1e
Tibia	Distal tibia transversal diameter	TTDd	1e

Columns: bone (teeth, skull, femora, humerus and tibia), measurement, abbreviation of the measurement and figure.

resultant equations (Moncunill-Solé *et al.*, 2014). When the BM estimation models were applied to the fossil register, the results were corrected by a logarithmic correction factor [the detransformed predicted values of each equation (values of BM) were multiplied by ration estimation, RE] (Smith, 1993). For each specific measurement the models calculated the average of individuals, and for the species the BM was estimated by a simple average ($\bar{X}$) and a geometric mean ($\bar{X}_G$) using the different measurements. The statistical analyses were performed with the IBM SPSS Statistics 19 software [Property of SPSS, Inc. (Chicago, IL, USA) and IBM Company (Armonk, NY, USA)].

The average of multiple individuals was used to create the models to avoid confusing intra- and interspecific allometry. Data of males and females were not analyzed separately because sexual dimorphism is insignificant in Lagomorpha (Lu, 2003). The specialized skeletal adaptations of forelimbs and hindlimbs, reflecting positional behavior and locomotion, can bring background noise to the regression models. Lagomorpha presents quadrupedal locomotion ranging from fast running to leaping. The analogous morphotype of the family of Leporidae is cursorial but with variation in running ability: (1) less cursorial with some degree of fossorial adaptation; (2) highly cursorial adapted to fast running and long leaps (López-Martínez, 1985; Fostowicz-Frelik, 2007). Fast runners present elongation of the distal segments of limbs (forearm and shank) and the proximal and medial phalanges, and shortening of the proximal segments, a part of the slimming of the shafts (Hildebrand, 1974). Similarly, pikas can be divided in two groups: (1) burrowers, living in steppe, forest or shrub habitats; (2) talus dwellers inhabiting boulder, talus or scree fields, and are generally non-burrowing leaper species. Burrowers present locomotor adaptations for digging in the scapula and humerus, while leapers have a longer tibial crest (Reese, Lanier & Sargis, 2013). The two families also differ in tooth morphology (López-Martínez, 1989). For this reason, we test the difference between families (ochotonids and leporids) for all variables except for those related with locomotion (length of long postcranial bones and diameters of the humerus), because the phylogeny is implicit in the locomotion groups. The following groups in relation to phylogeny and locomotion behavior are recognized: Ochotonidae (*O*), Leporidae (*L*), burrowing ochotonids (*BO*), non-burrowing ochotonids (*NBO*), cursorial leporids (*CL*) and highly cursorial leporids (*HL*). The statistical differences of the split equations will be tested with an analysis of the covariance (ANCOVA) (Supporting Information Appendix S1) and we will only show the regression models with significant differences. In the case of variables split by locomotion, we also show a model with all species (*A*) because probably the locomotor habits are unknown in fossil species.

Nesolagus netscheri and *Pentalagus furnessi*, both insular species, and *Caprolagus hispidus*, a species living in tall-grass savannahs, do not present the typical cursorial locomotion of leporids. Insular ecosystems without terrestrial predators and dense subtropical forests trigger low cursorial abilities, constraining capabilities for high-speed locomotion. This is the reason why we did not include them in 'cursorial leporids'.

The models created are codified by the measurement followed by a dash and the abbreviation of which sample the models are constructed from.

Table 3 Teeth and skull simple regression models for the estimation of body mass in Lagomorpha

Measurement	*N*	a	b	*P*-value	r^2	SEE	%PE	MAPE	RE	HV	CVr	Comments
Teeth												
WM/1-*L*	24	1.778	2.959	0.000	0.832	0.115	20.201	2.711	1.039	✓	0.896	$D_i < 1$
WM/1-*O*	12	1.483	2.728	0.000	0.852	0.068	9.999	2.020	1.010	✓	0.896	$D_i < 1$
LM/1-*L*	23	1.807	3.353	0.000	0.757	0.126	21.492	2.901	1.035	✓	0.839	*Brachylagus idahoensis* $D_i > 1$
LM/1-*O*	11	1.514	2.608	0.000	0.722	0.074	11.896	2.249	1.012	✓	0.752	*Ochotona cansus* Di > 1
M/1AA-*L*	24	1.890	1.470	0.000	0.815	0.120	21.092	2.596	1.043	✓	0.876	$D_i < 1$
M/1AA-*O*	11	1.454	1.418	0.000	0.790	0.065	10.702	2.082	1.010	✓	0.810	*O. cansus* Di > 1
TRL-*L*	30	0.547	2.247	0.000	0.668	0.151	29.133	3.917	1.049	✓	0.789	$D_i < 1$
TRL-*O*	12	−0.228	2.741	0.000	0.896	0.056	10.702	2.082	1.009	✓	0.927	$D_i < 1$
TRAA-*L*	23	0.462	1.659	0.000	0.808	0.112	19.928	2.676	1.029	✓	0.876	*B. idahoensis* $D_i > 1$
TRAA-*O*	12	0.566	1.397	0.000	0.893	0.057	9.336	1.848	1.009	✓	0.925	$D_i < 1$
Skull												
WOC-*A*	35	−1.526	4.091	0.000	0.957	0.115	21.331	3.238	1.034	✓	0.976	$D_i < 1$

Measurements (first column) used in the model (acronyms described in the text) are followed by a dash and another letter. This letter indicates with which sample the models are performed and have to be used (*A*, all sample; *BO*, burrower ochotonids; *L*, Leporidae; *O*, Ochotonidae). The following columns are: *N* (sample), a (constant of the model), b (allometric coefficient of X), *P*-value (significance < 0.05), r^2 (coefficient of determination), SEE (standard error of the estimation), %PE (average absolute per cent prediction), MAPE (mean absolute per cent prediction error), RE (ratio estimation), HV (ticked with homogeneity of the variances), CVr (correlation of cross-validation test) and Comments [Cook's distance (D_i), species with $D_i > 1$ were eliminated and the model was reconstructed again].

Results

Results of the regression models are in Tables 3–5 and Supporting Information Figure S1. Results of BM estimations of fossil lagomorphs are in Table 6.

Simple models

Teeth models were constructed split into families, leporids (*L*) and ochotonids (*O*) (ANCOVA $P < 0.05$), and offer significant results for all variables (r^2 ranges between 0.7 and 0.9). WOC, the only skull measurement of the study, shows an r^2 of 0.957 (ANCOVA $P > 0.05$), higher than the teeth models but with similar accuracy (SEE = 0.115). Cross-validations of dental and cranial measurements show suitability for most of the models ($r > 0.8$) with exception of LM/1-*O* and TRL-*L* (Table 3). Postcranial models were split in groups by phylogeny except for those measurements related with locomotion (see Materials and methods section). The ANCOVA analyses only showed significant differences between groups when we dealt with humerus diameters ($P < 0.05$). Femur models were performed with all lagomorph species (*A*) obtaining high coefficients of determination for each measurement. The humerus models, except *HL*, were constructed for locomotion groups as well as for all the species (*A*). The *A* humerus models have high coefficients of determination ($r^2 > 0.92$), while the split ones have lower coefficients but more precise estimations (SEE < 0.09). The *NBO* models for humerus parameters are not presented because the BM range of these species is very narrow, and the model is not realistic nor useful. In the case of the tibia, we performed only models with all species (*A*). The epiphyseal dimensions and the length offer high coefficients of determination. Cross-validations show suitability for all the postcranial models ($r > 0.91$) with the exception of HTDd-*BO* ($r = 0.858$) (Table 4).

Multiple models

Four different multiple regression models were done with (1) femur variables; (2) humerus variables; (3) femur and humerus variables; (4) femur, humerus, teeth and skull variables, using the entire species sample (48 species, excepting the fourth model). Dealing with femur variables, FTDd and FTDp were selected (first model), while for the humerus the variables HAPDd and HTDd were chosen (second model). The variability explained by the model is important in both cases ($r^2 = 0.97$), and both have high accuracy (SEE < 0.088). The third model (femur and humerus) was constructed with two variables (FTDd and HAPDd), without improving the accuracy and r^2 from the previous multiple models. Finally, the most integrative analysis selected two variables (FTDp and WOC). The variability explained increases to some degree ($r^2 = 0.979$), as well as the precision (SEE = 0.082). Cross-validations of multiple analyses were satisfactory in all cases (Table 5).

BM estimations

Fossil remains of *Prolagus* sp. and *N. rex* were used to estimate their BMs. The scarcity of fossil lagomorph remains limits our study sample size.

Only teeth and femora of *P. apricenicus* were available (Table 1). The fragmentation of all femora impedes the use of length as an estimator, and only epiphyseal diameters could be

Table 4 Postcranial simple regression models for the estimation of body mass in Lagomorpha

Measurement	*N*	a	b	*P*-value	r^2	SEE	%PE	MAPE	RE	HV	CVr	Comments
Femur												
FL-*A*	48	−1.110	2.229	0.000	0.961	0.102	19.080	2.757	1.020	✓	0.979	$D_i < 1$
FTDp-*A*	48	0.498	2.217	0.000	0.970	0.089	16.747	3.359	1.005	✓	0.984	$D_i < 1$
FTDd-*A*	48	0.318	2.481	0.000	0.970	0.089	16.361	2.408	1.011	✓	0.980	$D_i < 1$
FAPDd-*A*	48	0.225	2.630	0.000	0.954	0.111	20.331	2.961	0.994	✓	0.973	$D_i < 1$
Humerus												
HL-*A*	48	−1.221	2.418	0.000	0.949	0.117	22.749	3.170	1.003	✓	0.972	$D_i < 1$
HAPDp-*A*	48	0.270	2.819	0.000	0.952	0.114	21.862	3.236	0.995	✓	0.982	$D_i < 1$
HAPDp-*BO*	4	0.916	1.769	0.039	0.924	0.064	8.636	1.752	1.008	✓	0.910	$D_i < 1$
HAPDp-*L*	36	0.949	2.191	0.000	0.876	0.086	17.080	2.244	1.013	✓	0.939	$D_i < 1$
HTDd-*A*	48	−0.063	3.386	0.000	0.912	0.153	28.652	4.462	1.000	✓	0.973	$D_i < 1$
HTDd-*BO*	4	1.053	1.513	0.018	0.964	0.044	6.685	1.395	1.005	✓	0.858	$D_i < 1$
HTDd-*L*	36	0.934	2.393	0.000	0.875	0.087	15.997	2.144	1.013	✓	0.922	$D_i < 1$
HAPDd-*A*	48	1.130	2.553	0.000	0.967	0.093	17.792	2.595	0.991	✓	0.951	$D_i < 1$
HAPDd-*BO*	4	1.354	1.769	0.022	0.957	0.048	7.532	1.582	1.006	✓	0.925	$D_i < 1$
HAPDd-*L*	36	1.536	2.076	0.000	0.894	0.079	14.871	1.952	1.012	✓	0.927	$D_i < 1$
Tibia												
TL-*A*	45	−1.271	2.254	0.000	0.930	0.136	27.826	3.909	1.011	✓	0.961	$D_i < 1$
TTDp-*A*	45	0.219	2.577	0.000	0.976	0.080	14.353	2.146	1.010	✓	0.978	$D_i < 1$
TAPDp-*A*	45	0.599	2.265	0.000	0.960	0.103	19.429	2.662	1.004	✓	0.984	$D_i < 1$
TTDd-*A*	44	0.461	2.584	0.000	0.970	0.089	15.427	2.248	1.013	✓	0.986	$D_i < 1$

Measurements (first column) used in the model (acronyms described in the text) are followed by a dash and another letter. This letter indicates with which sample the models are performed and have to be used (*A*, all sample; *BO*, burrower ochotonids; *L*, leporidae; *O*, ochotonidae). The following columns are: *N* (sample), a (constant of the model), b (allometric coefficient of X), *P*-value (significance < 0.05), r^2 (coefficient of determination), SEE (standard error of the estimation), %PE (average absolute per cent prediction), MAPE (mean absolute per cent prediction error), RE (ratio estimation), HV (ticked with homogeneity of the variances), CVr (correlation of cross-validation test) and Comments [Cook's distance (D_i), species with $D_i > 1$ were eliminated and the model was reconstructed again].

Table 5 Multiple regression models for the estimation of body mass in Lagomorpha

Measurement	Model	*N*	a	b_1	*P*-value	r^2	SEE	%PE	MAPE	RE	HV	CVr	Comments
Multiple models													
FTDd-*A*	I	48	0.388	1.317	0.000	0.974	0.084	15.316	2.218	1.009	✓	0.985	$D_i < 1$
FTDp-*A*	–	–	–	1.054	–	–	–	–	–	–	–	–	–
HAPDd-*A*	II	48	1.576	3.404	0.000	0.971	0.088	16.591	2.383	0.994	✓	0.984	$D_i < 1$
HTDd-*A*	–	–	–	−1.182	–	–	–	–	–	–	–	–	–
FTDd-*A*	III	48	0.647	1.436	0.000	0.975	0.083	15.141	2.232	1.003	✓	0.985	$D_i < 1$
HAPDd-*A*	–	–	–	1.095	–	–	–	–	–	–	–	–	–
FTDp-*A*	IV	35	−0.205	1.505	0.000	0.979	0.082	15.701	2.35	1.017	✓	0.987	$D_i < 1$
WOC-*A*	–	–	–	1.360	–	–	–	–	–	–	–	–	–

Measurements (first column) used in the model (acronyms described in the text) are followed by a dash and another letter. This letter indicates with which sample the models are performed and have to be used (*A*, all sample). The fourth models (I, II, III and IV) have two variables (in the same model in different rows). The following columns are: *N* (sample), Model (number of model), a (constant of the model), b (allometric coefficient of X), *P*-value (significance < 0.05), r^2 (coefficient of determination), SEE (standard error of the estimation), %PE (average absolute per cent prediction), MAPE (mean absolute per cent prediction error), RE (ratio estimation), HV (ticked with homogeneity of the variances), CVr (correlation of cross-validation test) and Comments [Cook's distance (D_i), species with $D_i > 1$ were eliminated and the model was reconstructed again].

measured. Length, width and area of the first lower molar were also measured, but no other parameters were available for measuring. Weight estimation results were quite different, with lower results when we used teeth than when we used femoral parameters. Taking into account all the estimations we obtained a mean weight of 426.70 g, but considering only the postcranial material the estimation is around 600 g (Table 6, Fig. 2-1a/2a).

For estimating the weight of *P*. cf. *calpensis*, we had both teeth and postcranial bones (Table 1). The high level of fragmentation of long bones, the postmortem loss of molars and premolars, and the late fusion of some epiphyses checked the use of some parameters for estimating BM or significantly reduced the available sample. The results were variables with two important tendencies: (1) femur and tibia; (2) teeth and humerus. The general model's mean BM was 244.99 g while

Table 6 Body mass estimations of fossil lagomorphs: *Prolagus apricenicus*, *Prolagus* cf. *calpensis* and *Nuralagus rex*

	P. apricenicus		*P.* cf. *calpensis*		*N. rex*	
WM/1	286.59 (246.04–327.14)	*n* = 18	194.78 (161.72–227.85)	*n* = 27	–	–
LM/1	216.24 (199.32–233.17)	*n* = 19	133.07 (119.98–146.16)	*n* = 27	–	–
M/1AA	254.38 (228.24–280.51)	*n* = 18	159.22 (137.87–180.57)	*n* = 27	–	–
TRL	–	–	199.25 (62.70–335.79)	*n* = 2	4540.15 (4179.39–4900.91)*	*n* = 20
TRAA	–	–	181.69 (11.09–352.29)	*n* = 2	–	–
FTDp	658.80 (612.86–704.73)	*n* = 14	369.32 (312.00–426.64)	*n* = 4	7188.46 (6939.12–7437.80)	*n* = 17
FTDd	553.92 (505.49–602.35)	*n* = 9	300.51	*n* = 1	8484.04 (8182.14–8785.95)	*n* = 16
FAPDd	590.26 (549.05–631.46)	*n* = 10	403.69	*n* = 1	6343.49 (6001.08–6685.90)	*n* = 17
HAPDp-*A*	–	–	185.09 (117.60–252.60)	*n* = 2	–	–
HAPDp-*BO/L*	–	–	148.75 (114.50–183.00)*	*n* = 2	8440.26 (7855.29–9025.23)	*n* = 5
HTDd-*A*	–	–	231.05 (217.60–244.50)	*n* = 80	–	–
HTDd-*BO/L*	–	–	136.73 (133.20–140.30)*	*n* = 80	18 757.70 (18 042.33–19 473.06)*	*n* = 28
HAPDd-*A*	–	–	227.10 (211.50–242.70)	*n* = 84	–	–
HAPDd-*BO/L*	–	–	160.64 (154.00–167.30)*	*n* = 84	8436.60 (7986.48–8886.72)	*n* = 28
TTDp	–	–	281.60	*n* = 1	10 037.88 (9324.74–10 751.02)	*n* = 16
TAPDp	–	–	263.44 (246.90–279.99)	*n* = 2	5800.13 (5374.12–6226.15)	*n* = 15
TTDd	–	–	300.08 (273.07–327.08)	*n* = 10	10 801.08 (10 340.60–11 261.57)	*n* = 8
Mean	426.70	*n* = 6	244.99	*n* = 14	8241.49	*n* = 8
Mean_G	387.69	*n* = 6	233.67	*n* = 14	8078.73	*n* = 8
Mean FTi	600.99	*n* = 3	319.77	*n* = 6	–	–
Mean_G FTi	599.44	*n* = 3	316.09	*n* = 6	–	–
Mean TeH	252.40	*n* = 3	188.39	*n* = 6	–	–
Mean_G TeH	250.74	*n* = 3	184.99	*n* = 6	–	–

First column: model used to estimate the body mass (acronyms described in Table 2). For each estimation, we show the confidence interval (IC, calculated following Moncunill-Solé *et al.*, 2014) and the sample (*n*) that we used. Last rows are the means of the species where M is the arithmetic mean and M_G is the geometric mean. Different averages were done with different parameters (FTi = femora and tibia values; TeH = teeth and humerus values). Values in asterisk are not used to calculate the mean (see the text).

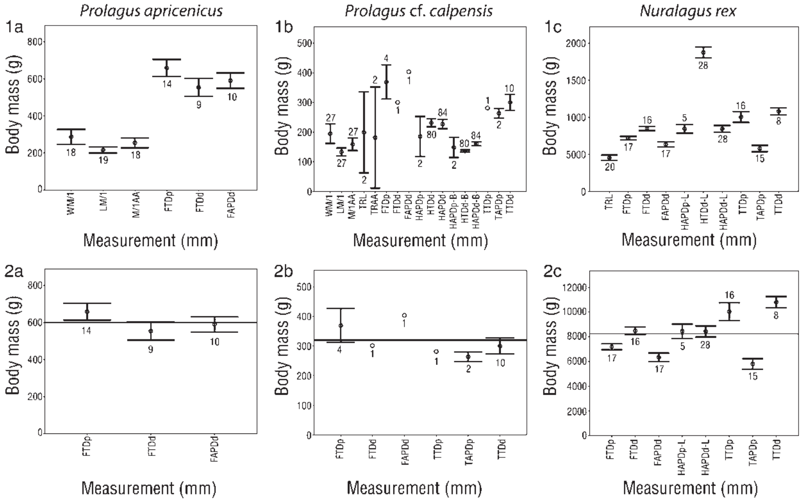

Figure 2 Graphics of body mass estimation results of the three fossil species (a) *Prolagus apricenicus*, (b) *Prolagus* cf. *calpensis* and (c) *Nuralagus rex*, representing each weight calculation (y axis) per estimator (x axis). The number below or under estimation is the sample of individuals used. The first row (1) contains all estimations performed, the second row (2) contains the estimations considered correct, the mean by a simple line.

the mean of the femur-tibia model was 319.77 g, and the teeth-humerus model was estimated to be 188.39 g (TRL-*O* and TRAA-*O* excluded, see below) (Table 6, Fig. 2-1b/2b).

The measurements for estimating the BM of *N. rex* are from Quintana Cardona (2005). Data came from postcranial measurements and only one dental parameter (TRL). Postcranial bones provided homogeneous results (excepting

HTDd), but TRL presents clearly lower values. For this reason, these two parameters were excluded for the average estimation (see below). The BM of the species was around 8241.49 g (Table 6, Fig. 2-1c/2c).

Discussion

BM estimation models for Lagomorpha

The most habitual measurements used to estimate BM of mammals are dental variables (length, width or area, particularly of the lower M1), for their easy determination and high abundance in the fossil record (Hopkins, 2008). However, postcranial bones, in contrast to dental parameters, are involved in weight bearing and, thus, provide more reliable BM estimations. In particular, diameters or perimeters of postcranial bones predict the BM of fossil mammals better than length parameters with few exceptions, see below (Legendre & Roth, 1988; Scott, 1990; Mendoza *et al*., 2006; Millien & Bovy, 2010). Our study is the first to offer allometric models for predicting BM in the Lagomorpha, including both Leporidae and Ochotonidae.

The obtained allometric models for estimating BM of lagomorphs are satisfactory in all cases, with high r^2 and low SEE and %PE (high accuracy). Nevertheless, teeth models are weaker, with lower r^2 and higher %PE than those obtained from postcranial parameters, confirming their expected lower relationship with BM (Legendre & Roth, 1988; Scott, 1990). Results of the WOC parameter are remarkable both in bivariate models and multiple-variable ones. This high correlation has already been observed in previous studies (Moncunill-Solé *et al*., 2014), although its use as an estimator will only be occasional because of the infrequent preservation of fossil skulls. On the other hand, postcranial bones offer the best models, as could be expected (Legendre & Roth, 1988; Scott, 1990; Mendoza *et al*., 2006; Millien & Bovy, 2010). We do not observe, as is reported in other studies (Scott, 1990), that length models are worse. Our results show that in some cases length models are better than epiphyseal ones. Femur, humerus and, unexpectedly, tibia models provided similar results despite the zeugopodial position of tibia. Zeugopods are more modified by locomotor specializations and preferences of the animal and do not only reflect its weight (Scott, 1990). Nevertheless, for BM estimations of the fossil lagomorph (*N. rex*), these tibia models present larger confidence intervals than the femur and humerus models. For this reason, we recommend the use of femora and humeri rather than tibiae. Our results also show that the variability explained (r^2) for specific models (dealing with humerus epiphysis) is lower than for general ones (*A* models), but they also present accurate predictions (lower SEE and %PE).

Multiple models provide slightly better results and more accuracy than simple regressions. However, sediments with fossil lagomorphs are generally washed and sifted (López-Martínez, 1989), leading to bone fragmentation and to separation of fragments of the same individual. This kind of fossil material hampers the use of multiple models and so the bivariate regressions are most often used. Simple models are constrained by ecological adaptations and phylogenetic legacy, but multiples compensate for these by using several measurements without redundant information (stepwise methodology) (Mendoza *et al*., 2006). Our fossil material (broken and without anatomical connection) did not allow the use of multiple models.

Using BM models in the fossil register

The two species of *Prolagus* differed importantly in their BMs because of their dwelling in different ecosystems: *P. apricenicus* was an insular giant form, one of the largest *Prolagus* species hitherto known (Angelone, 2007), while *P*. cf. *calpensis* was a typical mainland pika (Gil & Sesé, 1984; López-Martínez, 1989). Although they lived in different environments, we observed similar trends in the parameters used for BM estimations. The results show clearly lower predictions when using teeth (WM/1, LM/1, M/1AA, TRL and TRAA) compared with postcranial material. *Prolagus* is characterized by distinctive tooth morphology, having the lower M3 coalesced with the M2 (Dawson, 1969). This derived trait entails that *Prolagus* might not follow the general allometry of tooth dimensions and body size of typical lagomorphs. Furthermore, the teeth are not the better BM estimators, as their models are weaker (Table 3). Therefore, it is clear that, in the case of *Prolagus*, BM estimations using teeth are not reliable. The humerus estimations of *P*. cf. *calpensis* are surprisingly in line with the results from teeth, especially given the large sample of humeri measured in this species. Our *P*. cf. *calpensis* material is clearly biased toward a larger number of fused distal epiphyses of humeri (around 80 humeral epiphyses in contrast to the sample of fused femora and tibiae, which is 1 and 10, respectively). However, the material contains a large number of unfused femora, tibiae and proximal humeri from juveniles. It seems reasonable to think that the overrepresentation of fused distal epiphyses of humeri in contrast to the other postcranial bones may be the consequence of the sequence of growth plate fusion in lagomorphs. Differences in the fusion of growth plates in Lagomorpha have been previously reported (Taylor, 1959). Therefore, femora (fused later temporarily) would be more closely related with the adult body size than humeri, and, on this basis, we have to disregard these humeri estimations, too. It is important to be careful in interpreting obtained estimations, and preferably contrast them with different parameters. Ultimately, the BM estimation of *P. apricenicus* was around 600 g (Fig. 2-2a), and of *P*. cf. *calpensis* around 300 g (Fig. 2-2b).

N. rex, the giant insular leporid, provided BM estimations that are congruent with each other, with some exceptions. The TRL estimation is clearly lower than the others. Insularity might have caused a specific evolution of the dentition in *N. rex*, as it has in other mammals (Freudenthal, 1976; Moyà-Solà & Köhler, 1997), which does not support the usual allometric relationship between teeth and weight in Lagomorpha. This prompted us to remove dental parameters from the mean BM of the species. The HTDd parameter presents a surprisingly large estimation. Insular mammals develop traits for searching fallback foods under low resource conditions, presenting adaptations for digging and scrabbling the ground and a more specialized dentition for its abrasive diet (Köhler, 2010; Jordana *et al.*, 2012). Fossorial rodents and other mammals are characterized by a broad and robust distal humerus (Samuels & Valkenburgh, 2008; Rose & Lucas, 2000). The humeri of *N. rex* present some traits for improving its skills for the fossorial lifestyle (Quintana *et al.*, 2011). The tight relationship of HTDd with the digging lifestyle indicates that it is not a reliable estimator, and we have decided to exclude these estimations. Our results suggest for *N. rex* a weight of around 8000 g (min/max: 6343.49/10 801.08), which contrasts with previous estimations of 12 000 g (min/max: 9254/14 498) (Quintana *et al.*, 2011). Our study is more reliable because it increases the number of species with which *N. rex* BM models are constructed, and because we used more parameters to test its weight. However, the large size of *N. rex* calls for caution in applying regression models created with extant lagomorphs where the largest weight is around 5000 g (*Lepus arcticus*). Extrapolating beyond the range of extant data to make predictions entails wariness in interpreting the results (Quinn & Keough, 2002; Millien, 2008).

The direct comparison of two species of the *Prolagus* genus, one from an insular ecosystem and the other from the mainland, permits us to identify a heavier pika on the Gargano paleoisland. *Prolagus apricenicus* is the smaller and more primitive of the two pikas at the island's karstic site, presenting morpho-dimensional modifications over time due to its isolation (Angelone, 2007). *Prolagus imperialis* Mazza, 1987 inhabited the Gargano paleoisland too, but in its youngest fissures, coexisting with *P. apricenicus*, and it was characterized by its enormous size (Masini *et al.*, 2010). BM changes in insular endemic faunas are triggered by the peculiar ecological pressures that govern insular ecosystems (low extrinsic mortality and limited resources) (Palkovacs, 2003). In comparison, *P.* cf. *calpensis* was from the mainland and shared its ecosystem with other micromammals, principally rodents (Gil & Sesé, 1984), and large mammals (Soto & Morales, 1985). The presence of carnivores (ursids, hyenids and felids) in Casablanca I suggests a high predation pressure on *P.* cf. *calpensis*, as has been observed in current ecosystems (Valverde, 1964). Predation pressure was lower at the Gargano site (Masini *et al.*, 2010), and may account for the larger size *P. apricenicus* or *P. imperialis*. On the other hand, *N. rex* had an exceptionally large BM for a leporid. The Minorcan rabbit dwelled on a small island, sharing the resources and space with only another mammal, the dormouse *Muscardinus cyclopeus* Agustí, Moyà-Sola & Pons Moyà, 1982 (Bover, Quintana & Alcover, 2008). This simple ecosystem contrasts with the complex structure of the mammalian fauna of Gargano. We cannot make direct comparisons between *N. rex* and *P. apricenicus*, although both are insular species. Pikas, in all cases, present ranges of BMs lower than leporids, leading us to suggest that phylogenetic constraints would have played an important role.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. ANCOVA analyses of the variables (body mass and some skeletal measurement) in relation to their phylogeny or locomotion. For more references, see the text.

Figure S1. Bivariate regression models in log-log created between body mass (BM) and: (A) WM/1; (B) LM/1; (C) M/1AA; (D) TRL; (E) TRAA; (F) WOC; (G) FL; (H) FTDp; (I) FTDd; (J) FAPDd; (K) HL; (L) HAPDp for all species; (M) HAPDp for Leporidae and burrower Ochotonidae species; (N) HTDd for all species; (O) HTDd for Leporidae and burrower Ochotonidae species; (P) HAPDd for all species; (Q) HAPDd for Leporidae and burrower Ochotonidae species; (R) TL; (S) TTDp; (T) TAPDp; (U) TTDd. Leporids are represented by black points (●) and ochotonids by white ones (○).

Table S1. Extant Lagomorpha material for performing the body mass estimation models (36 of the 61 extant species of leporids and 12 of the 30 species of extant ochotonids were measured). The species are ordered by family and then by species. The following columns are the type of locomotion (superscript star: they are not used when models by locomotion are developed, see Materials and methods section), the museum (or from which literature we obtain the data), the sample (N), the mean body mass for the species (g), and the body mass literature (all the body mass data are from literature, except those obtained from specimens of the Institute of Zoology from the Chinese Academy of Sciences). The species *Pronolagus rupestris* is repeated because we use the measurements of humerus from Quintana Cardona (2005) and the rest of measurements from the material measured in the Smithsonian Institution.

Appendix S1. Ancova analyses of the variables (body mass and some skeletal measurement) in relation to their phylogeny or locomotion. For references, see the text.

ANCOVA group by PHYLOGENY

Variable: WM/1

Factores inter-sujetos

		N
FAMILY_N	Leporidae	24
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	10,065[a]	2	5,033	493,283	,000	,968	986,566	1,000
Intersección	3,648	1	3,648	357,582	,000	,916	357,582	1,000
LogWM1	1,692	1	1,692	165,810	,000	,834	165,810	1,000
FAMILY_N	,346	1	,346	33,939	**,000**	,507	33,939	1,000
Error	,337	33	,010					
Total	305,431	36						
Total corregida	10,402	35						

a. R cuadrado = ,968 (R cuadrado corregida = ,966)

b. Calculado con alfa = ,05

Variable: LM/1

Factores inter-sujetos

		N
FAMILY_N	Leporidae	24
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	9,908[a]	2	4,954	330,646	,000	,952	661,292	1,000
Intersección	6,785	1	6,785	452,853	,000	,932	452,853	1,000
LogLM1	1,534	1	1,534	102,383	,000	,756	102,383	1,000
FAMILY_N	1,516	1	1,516	101,189	**,000**	,754	101,189	1,000
Error	,494	33	,015					
Total	305,431	36						
Total corregida	10,402	35						

a. R cuadrado = ,952 (R cuadrado corregida = ,950)

b. Calculado con alfa = ,05

Variable: M/1AA

Factores inter-sujetos

		N
FAMILY_N	Leporidae	24
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	10,027[a]	2	5,014	441,560	,000	,964	883,120	1,000
Intersección	4,754	1	4,754	418,685	,000	,927	418,685	1,000
LogM1AA	1,654	1	1,654	145,638	,000	,815	145,638	1,000
FAMILY_N	,740	1	,740	65,177	**,000**	,664	65,177	1,000
Error	,375	33	,011					
Total	305,431	36						
Total corregida	10,402	35						

a. R cuadrado = ,964 (R cuadrado corregida = ,962)

b. Calculado con alfa = ,05

Variable: TRL

Factores inter-sujetos

		N
FAMILY_N	Leporidae	36
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	10,889[a]	2	5,444	255,467	,000	,919	510,934	1,000
Intersección	,125	1	,125	5,881	,019	,116	5,881	,660
LogTRL	1,490	1	1,490	69,917	,000	,608	69,917	1,000
FAMILY_N	,528	1	,528	24,792	**,000**	,355	24,792	,998
Error	,959	45	,021					
Total	428,747	48						
Total corregida	11,848	47						

a. R cuadrado = ,919 (R cuadrado corregida = ,915)

b. Calculado con alfa = ,05

Variable: TRAA

Factores inter-sujetos

		N
FAMILY_N	Leporidae	24
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	10,063[a]	2	5,031	489,414	,000	,967	978,829	1,000
Intersección	,178	1	,178	17,312	,000	,344	17,312	,981
LogTRAA	1,689	1	1,689	164,301	,000	,833	164,301	1,000
FAMILY_N	,233	1	,233	22,626	**,000**	,407	22,626	,996
Error	,339	33	,010					
Total	305,431	36						
Total corregida	10,402	35						

a. R cuadrado = ,967 (R cuadrado corregida = ,965)

b. Calculado con alfa = ,05

Variable: WOC

Factores inter-sujetos

		N
FAMILY	Leporidae	24
	Ochotonidae	11

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	9,773[a]	2	4,887	382,532	,000	,960	765,064	1,000
Intersección	,127	1	,127	9,979	,003	,238	9,979	,865
LogWOC	1,567	1	1,567	122,660	,000	,793	122,660	1,000
FAMILY	,029	1	,029	2,286	**,140**	,067	2,286	,311
Error	,409	32	,013					
Total	299,670	35						
Total corregida	10,182	34						

a. R cuadrado = ,960 (R cuadrado corregida = ,957)

b. Calculado con alfa = ,05

Variable: FTDp

Factores inter-sujetos

		N
FAMILY	Leporidae	36
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,936[a]	2	5,968	795,423	,000	,972	1590,845	1,000
Intersección	,259	1	,259	34,531	,000	,434	34,531	1,000
LogFTDp	2,018	1	2,018	268,931	,000	,857	268,931	1,000
FAMILY	,033	1	,033	4,428	**,051**	,090	4,428	,540
Error	,338	45	,008					
Total	435,109	48						
Total corregida	12,274	47						

a. R cuadrado = ,972 (R cuadrado corregida = ,971)

b. Calculado con alfa = ,05

Variable: FTDd

Factores inter-sujetos

		N
FAMILY	Leporidae	36
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,923[a]	2	5,962	765,998	,000	,971	1531,997	1,000
Intersección	,105	1	,105	13,499	,001	,231	13,499	,949
LogFTDd	2,005	1	2,005	257,637	,000	,851	257,637	1,000
FAMILY	,019	1	,019	2,484	**,122**	,052	2,484	,338
Error	,350	45	,008					
Total	435,109	48						
Total corregida	12,274	47						

a. R cuadrado = ,971 (R cuadrado corregida = ,970)

b. Calculado con alfa = ,05

Variable: FAPDd

Factores inter-sujetos

		N
FAMILY	Leporidae	36
	Ochotonidae	12

Pruebas de los efectos inter-sujetos

Variable dependiente:LogFAPDd

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	1,617[a]	2	,809	478,490	,000	,955	956,979	1,000
Intersección	,003	1	,003	1,730	,195	,037	1,730	,251
LogFAPDd	,351	1	,351	207,935	,000	,822	207,935	1,000
FAMILY	,002	1	,002	,947	**,336**	,021	,947	,159
Error	,076	45	,002					
Total	53,911	48						
Total corregida	1,693	47						

a. R cuadrado = ,955 (R cuadrado corregida = ,953)

b. Calculado con alfa = ,05

Variable: TTDp

Factores inter-sujetos

		N
FAMILY	Leporidae	35
	Ochotonidae	10

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,159[a]	2	5,579	932,662	,000	,978	1865,324	1,000
Intersección	,067	1	,067	11,130	,002	,209	11,130	,903
LogTTDp	1,968	1	1,968	328,952	,000	,887	328,952	1,000
FAMILY	,021	1	,021	3,512	**,068**	,077	3,512	,449
Error	,251	42	,006					
Total	415,468	45						
Total corregida	11,410	44						

a. R cuadrado = ,978 (R cuadrado corregida = ,977)

b. Calculado con alfa = ,05

Variable: TAPDp

Factores inter-sujetos

		N
FAMILY	Leporidae	35
	Ochotonidae	10

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	10,990[a]	2	5,495	548,769	,000	,963	1097,537	1,000
Intersección	,349	1	,349	34,862	,000	,454	34,862	1,000
LogTAPDp	1,799	1	1,799	179,627	,000	,810	179,627	1,000
FAMILY	,037	1	,037	3,721	**,061**	,081	3,721	,470
Error	,421	42	,010					
Total	415,468	45						
Total corregida	11,410	44						

a. R cuadrado = ,963 (R cuadrado corregida = ,961)

b. Calculado con alfa = ,05

Variable: TTDd

Factores inter-sujetos

		N
FAMILY	Leporidae	35
	Ochotonidae	10

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,159[a]	2	5,579	932,662	,000	,978	1865,324	1,000
Intersección	,067	1	,067	11,130	,002	,209	11,130	,903
LogTTDp	1,968	1	1,968	328,952	,000	,887	328,952	1,000
FAMILY	,021	1	,021	3,512	**,068**	,077	3,512	,449
Error	,251	42	,006					
Total	415,468	45						
Total corregida	11,410	44						

a. R cuadrado = ,978 (R cuadrado corregida = ,977)

b. Calculado con alfa = ,05

ANCOVA group by LOCOMOTION

Variable: FL (Three groups: Cursorial leporids, non-cursorial ochotnoids and runner leporids).

Factores inter-sujetos

		N
LOCOMOTION	C	21
	NC	12
	R	15

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,804[a]	3	3,935	368,448	,000	,962	1105,343	1,000
Intersección	,062	1	,062	5,763	,021	,116	5,763	,651
LogFL	1,173	1	1,173	109,887	,000	,714	109,887	1,000
LOCOMOTION	,010	2	,005	,477	**,624**	,021	,955	,123
Error	,470	44	,011					
Total	435,109	48						
Total corregida	12,274	47						

a. R cuadrado = ,962 (R cuadrado corregida = ,959)

b. Calculado con alfa = ,05

Variable: HL (Three groups: Cursorial leporids, non-cursorial ochotonids and runner leporids).

Factores inter-sujetos

		N
LOCOMOTION	C	20
	NC	12
	R	16

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	4,327[a]	3	2,163	171,681	,000	,953	343,361	1,000
Intersección	,085	1	,085	6,742	,019	,284	6,742	,687
LogHL	,891	1	,891	70,695	,000	,806	70,695	1,000
LOCOMOTION	,005	2	,005	,413	**,529**	,024	,413	,093
Error	,214	44	,013					
Total	168,283	48						
Total corregida	4,541	47						

a. R cuadrado = ,953 (R cuadrado corregida = ,947)

b. Calculado con alfa = ,05

Variable: HAPDp (Three groups: digger ochotonids, leporids and non-digger ochotonids).

Factores inter-sujetos

		N
LOCOMOTION	D	4
	L	36
	ND	7

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,657[a]	3	3,886	586,050	,000	,976	1758,150	1,000
Intersección	,376	1	,376	56,658	,000	,569	56,658	1,000
LogHAPDp	1,915	1	1,915	288,822	,000	,870	288,822	1,000
LOCOMOTION	,309	2	,154	23,284	**,000**	,520	46,567	1,000
Error	,285	43	,007					
Total	429,359	47						
Total corregida	11,942	46						

a. R cuadrado = ,976 (R cuadrado corregida = ,974)

b. Calculado con alfa = ,05

Variable: HTDd (Three groups: digger ochotonids, leporids and non-digger ochotonids).

Factores inter-sujetos

		N
LOCOMOTION	D	4
	L	36
	ND	8

Pruebas de los efectos inter-sujetos[c]

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	7,629[a]	2	3,814	90,013	,000	,800	180,026	1,000
Intersección	97,669	1	97,669	2304,823	,000	,981	2304,823	1,000
LOCOMOTION	7,629	2	3,814	90,013	**,000**	,800	180,026	1,000
Error	1,907	45	,042					
Total	407,973	48						
Total corregida	9,536	47						

a. R cuadrado = ,800 (R cuadrado corregida = ,791)

b. Calculado con alfa = ,05

c. Regresión de mínimos cuadrados ponderados - Ponderada por LogHTDd

Variable: HAPDd (Three groups: digger ochotonids, leporids and non-digger ochotonids).

Factores inter-sujetos

		N
LOCOMOTION	D	4
	L	36
	ND	7

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	11,704[a]	3	3,901	706,765	,000	,980	2120,294	1,000
Intersección	2,709	1	2,709	490,706	,000	,919	490,706	1,000
LogHAPDd	1,963	1	1,963	355,539	,000	,892	355,539	1,000
LOCOMOTION	,162	2	,081	14,658	**,000**	,405	29,315	,998
Error	,237	43	,006					
Total	429,359	47						
Total corregida	11,942	46						

a. R cuadrado = ,980 (R cuadrado corregida = ,979)

b. Calculado con alfa = ,05

Variable: TL (Three groups: Cursorial leporids, non-cursorial ochotonids and runner leporids).

Factores inter-sujetos

		N
LOCOMOTION	C	20
	NC	10
	R	15

Pruebas de los efectos inter-sujetos

Variable dependiente:LogBM

Origen	Suma de cuadrados tipo III	gl	Media cuadrática	F	Sig.	Eta al cuadrado parcial	Parámetro de no centralidad Parámetro	Potencia observada[b]
Modelo corregido	10,639[a]	3	3,546	188,426	,000	,932	565,279	1,000
Intersección	,050	1	,050	2,668	,110	,061	2,668	,358
LogTL	,786	1	,786	41,749	,000	,505	41,749	1,000
LOCOMOTION	,026	2	,013	,696	**,504**	,033	1,392	,159
Error	,772	41	,019					
Total	415,468	45						
Total corregida	11,410	44						

a. R cuadrado = ,932 (R cuadrado corregida = ,927)

b. Calculado con alfa = ,05

Figure S1. Bivariate regression models in log-log created between body mass (BM) and: (A) WM/1; (B) LM/1; (C) M/1AA; (D) TRL; (E) TRAA; (F) WOC; (G) FL; (H) FTDp; (I) FTDd; (J) FAPDd; (K) HL; (L) HAPDp for all species; (M) HAPDp for Leporidae and burrower Ochotonidae species; (N) HTDd for all species; (O) HTDd for Leporidae and burrower Ochotonidae species; (P) HAPDd for all species; (Q) HAPDd for Leporidae and burrower Ochotonidae species; (R) TL; (S) TTDp; (T) TAPDp; (U) TTDd. Leporids are represented by black points and ochotonids by white ones.

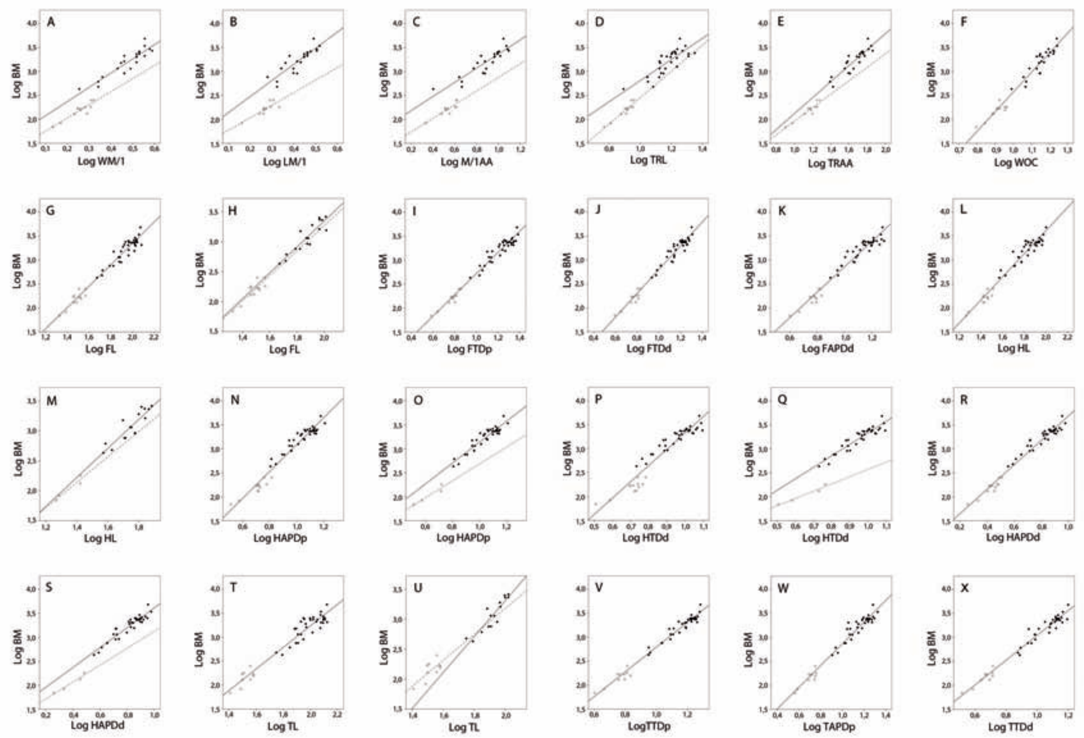

Table S1. Extant Lagomorpha material for performing the body mass estimation models (36 of 61 extant species of leporids and 12 of 30 species of extant ochotonids were measured). The species are ordered by family and then by species. The following columns are the type of locomotion (superscript star: they are not used when models by locomotion are developed, see Materials and methods section), the museum (or from which literature we obtain the data), the sample (N), the mean body mass for the species (g), and the body mass literature (all the body mass data are from literature, except those obtained from specimens of Institute of Zoology from the Chinese Academy of Sciences). The species *Pronolagus rupestris* is repeated because we use the measurements of humerus from Quintana Cardona (2005) and the rest of measurements from the material measured in the Smithsonian Institution.

FAMILY	SPECIES	LIFE STYLE	MUSEUM	SAMPLE (N)	MEAN BODY MASS (g)	BM LITERATURE
Leporidae	*Brachylagus idahoensis*	Cursorial	NMNH	10	428	Silva and Downing (2005)
Leporidae	*Bunolagus monticularis*	Cursorial*	Quintana (2005)	2	1250	Ernest (2003)
Leporidae	*Caprolagus hispidus*	Cursorial*	Quintana (2005)	1	2500	Ernest (2003)
Leporidae	*Lepus alleni*	Runner	NMNH	10	3400	Silva and Downing (2005)
Leporidae	*Lepus americanus*	Cursorial	NMNH	12	1550	Silva and Downing (2005)
Leporidae	*Lepus arcticus*	Highly cursorial	NMNH	10	4810	Silva and Downing (2005)
Leporidae	*Lepus californicus*	Highly cursorial	NMNH	10	2300	Silva and Downing (2005)
Leporidae	*Lepus callotis*	Highly cursorial	NMNH	10	2500	Silva and Downing (2005)
Leporidae	*Lepus capensis*	Highly cursorial	NMNH	10	2040	Silva and Downing (2005)
Leporidae	*Lepus castroviejoi*	Highly cursorial	Quintana (2005)	2	2830	Jones et al. (2009)
Leporidae	*Lepus crawshayi*	Highly cursorial	Quintana (2005)	3	2340	Silva and Downing (2005)
Leporidae	*Lepus granatensis*	Highly cursorial	Quintana (2005)	3	2330	Jones et al. (2009)
Leporidae	*Lepus oiostolus*	Highly cursorial	NMNH	11	2480	Jones et al. (2009)
Leporidae	*Lepus peguensis*	Highly cursorial	NMNH	11	2105	Silva and Downing (2005)
Leporidae	*Lepus saxatilis*	Highly cursorial	Quintana (2005)	5	2410	Silva and Downing (2005)
Leporidae	*Lepus tibetanus*	Highly cursorial	NMNH	10	1991.67	Institute of Zoology, Chinese Academy of Sciences
Leporidae	*Lepus timidus*	Highly cursorial	NMNH	10	2700	Silva and Downing (2005)
Leporidae	*Lepus tolai*	Highly cursorial	NMNH	17	2110	Ernest (2003)
Leporidae	*Lepus townsendii*	Highly cursorial	NMNH	15	2910	Silva and Downing (2005)
Leporidae	*Nesolagus netscheri*	Cursorial*	Quintana (2005)	1	1520	Jones et al. (2009)
Leporidae	*Oryctolagus cuniculus*	Cursorial	Quintana (2005)	20	1896.43	Quintana (2005)
Leporidae	*Pentalagus furnessi*	Cursorial*	Quintana (2005)	4	2396.25	Smith et al. (2003)
Leporidae	*Poelagus marjorita*	Cursorial	Quintana (2005)	1	2500	Ernest (2003)
Leporidae	*Pronolagus crassicaudatus*	Cursorial	Quintana (2005) and SNMNH	4	2600	Silva and Downing (2005)
Leporidae	*Pronolagus randensis*	Cursorial	Quintana (2005)	2	2300	Silva and Downing (2005)
Leporidae	*Pronolagus rupestris*	Cursorial	NMNH	12	1620	Silva and Downing (2005)

Leporidae	*Pronolagus rupestris*	Cursorial	Quintana (2005)	4	1620	Silva and Downing (2005)
Leporidae	*Romerolagus diazi*	Cursorial	NMNH	9	477	Silva and Downing (2005)
Leporidae	*Sylvilagus aquaticus*	Cursorial	NMNH	10	2330	Silva and Downing (2005)
Leporidae	*Sylvilagus audubonii*	Cursorial	Quintana (2005)	18	756	Silva and Downing (2005)
Leporidae	*Sylvilagus bachmani*	Cursorial	NMNH	15	610	Silva and Downing (2005)
Leporidae	*Sylvilagus brasiliensis*	Cursorial	Quintana (2005)	2	1150	Silva and Downing (2005)
Leporidae	*Sylvilagus floridanus*	Cursorial	NMNH	8	1140	Silva and Downing (2005)
Leporidae	*Sylvilagus nuttallii*	Cursorial	NMNH	10	759.96	Ernest (2003)
Leporidae	*Sylvilagus obscurus*	Cursorial	NMNH	10	756-1083	Wilson and Ruff (1999)
Leporidae	*Sylvilagus palustris*	Cursorial	NMNH	10	1500	Silva and Downing (2005)
Leporidae	*Sylvilagus transitionalis*	Cursorial	NMNH	16	902.6	Ernest (2003)
Ochotonidae	*Ochotona argentata*	Leaper	NMNH	2	251.375	Institute of Zoology, Chinese Academy of Sciences
Ochotonidae	*Ochotona cansus*	Burrower	NMNH	10	68.75	Smith et al. (2003)
Ochotonidae	*Ochotona collaris*	Leaper	NMNH	10	129	Ernest (2003)
Ochotonidae	*Ochotona curzoniae*	Burrower	NMNH	9	131.475	Smith et al. (2003)
Ochotonidae	*Ochotona erythrotis*	Leaper	NMNH	3	181	Smith et al. (2003)
Ochotonidae	*Ochotona gloveri*	Leaper	NMNH	8	156.2	Institute of Zoology, Chinese Academy of Sciences
Ochotonidae	*Ochotona ladacensis*	Burrower	NMNH	10	179.35	Institute of Zoology, Chinese Academy of Sciences
Ochotonidae	*Ochotona macrotis*	Leaper	NMNH	15	167	Ernest (2003)
Ochotonidae	*Ochotona princeps*	Leaper	NMNH	9	169.5	Silva and Downing (2005)
Ochotonidae	*Ochotona roylei*	Leaper	NMNH	11	168.5	Silva and Downing (2005)
Ochotonidae	*Ochotona rufescens*	Intermediate	NMNH	16	250	Ernest (2003)
Ochotonidae	*Ochotona thibetana*	Burrower	NMNH	16	83.1	Smith et al. (2003)

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Chapter 7

Comparing the body mass variations in endemic insular species of *Prolagus* (Ochotonidae, Lagomorpha) in the Pleistocene of Sardinia (Italy)

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COMPARING THE BODY MASS VARIATIONS IN ENDEMIC INSULAR SPECIES OF THE GENUS *PROLAGUS* (OCHOTONIDAE, LAGOMORPHA) IN THE PLEISTOCENE OF SARDINIA (ITALY)

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Abstract. Prolagus figaro and *P. sardus* are part of an endemic insular anagenetic lineage that populated Sardinia since the earliest Late Pliocene to Holocene. BM of some populations of these two species was calculated using regression models. The best BM proxies for *Prolagus* are: femur length, zeugopod measurements and distal humerus diameter. The anagenetic lineage shows a BM increase of ca 20% from the populations of *P. figaro* (398-436 g) to *P. sardus* (504-525 g). The trend shown by the size of lower third premolar, even if not directly comparable with BM, is opposite (ca -30% at the transition *P. figaro-P. sardus*). Compared to *P.* cf. *calpensis*, a continental species of similar age, BM of *P. figaro* is ca +25%. The comparison with the insular endemic *P. apricenicus* evidenced differences in BM range and timespan required to attain it, due to the different size and palaeogeographical situation of the islands. Insular endemic *Prolagus* follow the small mammal pattern of Island Rule. Mein's (1983) biphasic model seems applicable to the evolution of *P. figaro*. A tachytelic phase followed by a bradytelic one seems to characterize also the appearance of *P. sardus*, at least for dental traits, a process probably triggered by important variations of abiotic and biotic traits of the environment, as indicated by the turnover that marks the onset of the Dragonara subcomplex. The prediction of life history traits and other biological attributes of Sardinian *Prolagus* using BM should be considered with caution due to the complexity of ecological selective regimes of Sardinia.

INTRODUCTION

Body size is a fundamental trait in the biology and ecology of species as it shows tight correlation with several physiological, behavioral, morphological, ecological and life history attributes (Peters 1983; Calder 1984). The best proxy for quantifying the BS of individuals is their body mass or weight (Gingerich et al. 1982). Thus, predicting the BM of fossil species is of critical significance for knowing their biology as well as for understanding and quantifying their adaptations to habitats (Palombo 2009a). For most of mammalian taxa, the allometric relationships among BM and bone/dental measurements of extant relative species allow the development of regression models to estimate the average weight of extinct ones (Damuth & MacFadden 1990; see Palombo 2009a: tab. 1 for a synopsis).

In spite of the abundance, diversity and ubiquity of fossil lagomorphs (leporids and ochotonids), models for estimating the BMs of species belonging to this order were developed very recently. Quintana Cardona (2005) and Quintana et al. (2011) provided the first models for leporids. Subsequently, expanding the database of Quintana Cardona (2005) and adding measurements of extant ochotonids, Moncunill-Solé et al. (2015) developed general and specific equations for estimating the BM of lagomorphs based on a multiproxy approach (teeth, cranial and postcranial measurements). BM estimation models for lagomorphs are going to enhance data about palaeocommunity structures and their palaeoenvironmental interpretations.

In view of the potential of this field, we decided to study the BM of the insular endemic ochotonids of the Pleistocene of Sardinia (Italy): *Prolagus figaro* and *Prolagus sardus*. *Prolagus figaro* is known from the latest Pliocene/earliest Pleistocene to the late Early Pleistocene of Sardinia (Capo Figari/

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		Femora	Tibiae	Humeri
Species	Fissure filling	N	N	N
		(coding)	(coding)	(coding)
Prolagus figaro	X3	10	6	14
		(SSN/X3/fe/1–10)	(SSN/X3/ti/1–6)	(SSN/X3/hu/1–14)
	IVm	5	–	–
		(SSN/IVm/fe/1–5)		
	X4	13	11	–
		(SSN/X4/fe/1–13)	(SSN/X4/ti/1–11)	
Prolagus sardus	XIr	74	42	60
		(SSN/XIr/fe/1–74)	(SSN/XIr/ti/1–42)	(SSN/XIr/hu/1–60)
	VI6	20	9	49
		(SSN/VI6/fe/1–20)	(SSN/VI6/ti/1–9)	(SSN/VI6/hu/1–49)

Tab. 1 - Fossil material used for performing the study.

Orosei 1 subcomplex of the *Nesogoral* FC- Orosei 2 subcomplex of the *Microtus* (*Tyrrhenicola*) FC; Palombo 2009b). *Prolagus sardus* is reported since the Middle Pleistocene (Dragonara subcomplex of the *Microtus* (*Tyrrhenicola*) FC; Palombo 2009b) until historical epoch in Sardinia and also in Corsica (Vigne & Valladas 1996; Wilkens 2004). We aim to:

1) Evaluate the BM trend of *Prolagus* in an insular habitat from an evolutionary point of view, as the two species of *Prolagus* from Sardinia are part of an anagenetic evolutionary lineage (Angelone et al. 2015).

2) Assess the response of fossil ochotonid species to insular regimes (Island Rule) (see Palombo 2009a and references therein for an update of the debate about this subject) as there are not extant relatives living on islands.

3) Provide data to increase the scarce biological knowledge of Sardinian *Prolagus*.

ABBREVIATIONS

BM: body mass; BS: body size; CMd1: Capo Mannu D1; IC: interval of confidence; FC: faunal complex; FL: femur length; FTDd: distal femoral transversal diameter; FTDp: proximal femoral transversal diameter; HAPDd: distal humeral anteroposterior diameter;

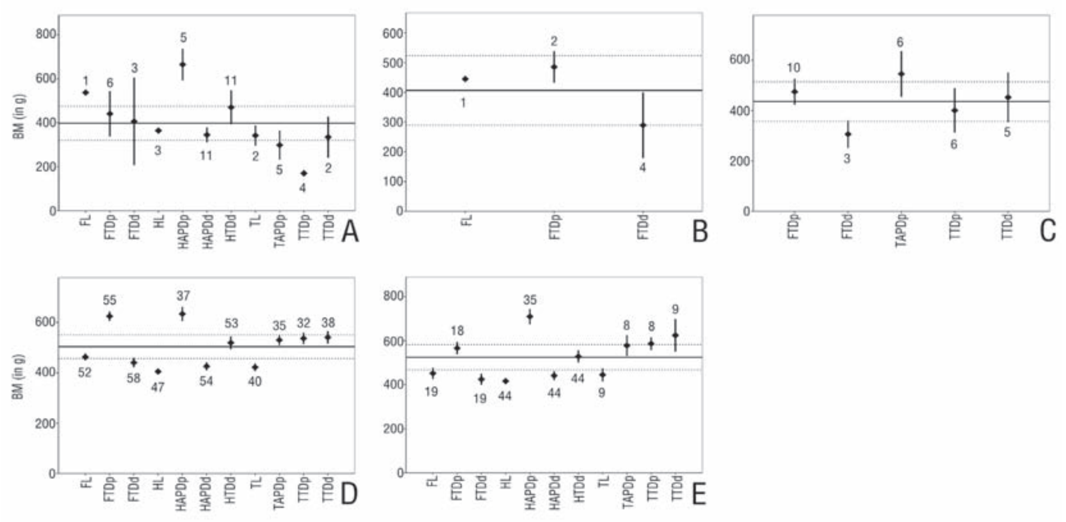

Fig. 1 - BM predictions (Y axis, in g) for *Prolagus figaro* and *P. sardus* calculated on the basis of different postcranial measurements (X axis). BM average (black line), confidence interval (dotted lines) and number of individuals are shown. A) *Prolagus figaro*, fissure infilling X3; B) *P. figaro,* fissure infilling IVm; C) *P. figaro*, fissure infilling X4; D) *Prolagus sardus*, fissure infilling XIr and E) *P. sardus*, fissure infilling VIb.

		BM *Prolagus figaro*						**BM *Prolagus sardus***			
		X3		**IVm**		**X4**		**XIr**		**VI6**	
Measurement	**Equation**	**$\bar{x}$**	**N**	**$\bar{x}$**	**N**	**$\bar{x}$**	**N**	**$\bar{x}$**	**N**	**$\bar{x}$**	**N**
		(IC)		**(IC)**		**(IC)**		**(IC)**		**(IC)**	
FL	logBM=−1.11+2.229logFL	537.57	1	444.74	1	−	−	463.09	52	452.12	19
								(448.98-477.20)		(426.38−477.85)	
FTDp	logBM=0.498+2.217logFTDp	441.19	6	484.96	4	474.51	10	624.91	55	566.28	18
		(337.88-544.51)		(432.23-537.69)		(423.18-525.84)		(605.96-643.86)		(538.47-594.08)	
FTDd	logBM=0.318+2.481logFTDd	406.21	3	289.40	2	306.13	3	440.50	58	424.84	19
		(207.12-605.30)		(178.91-399.90)		(251.76-360.51)		(421.79-459.21)		(398.98-450.70)	
HL	logBM=−1.221+2.418logHL	364.47	3	−	−	−	−	633.99	47	416.71	44
		(360.73-368.22)						(605.66-662.33)		(403.42-430.00)	
HAPDp	logBM=0.916+1.769logHAPDp	665.15	5	−	−	−	−	633.99	37	709.82	35
		(593.75-736.56)						(605.66-662.33)		(675.19-744.15)	
HAPDd	logBM=1.354+1.769logHAPDd	345.03	11	−	−	−	−	425.75	54	441.69	44
		(311.26-378.80)						(409.64-441.87)		(421.16-462.25)	
HTDd	logBM=1.053+1.513logHTDd	470.57	11	−	−	−	−	519.21	53	528.79	44
		(393.39-547.74)						(493.6-544.77)		(501.34-556.24)	
TL	logBM=−1.271+2.254logTL	342.28	2	−	−	−	−	422.18	40	445.57	9
		(296.52-388.03)						(407.09-437.27)		(415.82-475.32)	
TAPDp	logBM=0.599+2.265logTAPDp	298.77	5	−	−	545.27	6	530.28	35	578.26	8
		(233.38-364.16)				(454.86-635.69)		(509.28-551.47)		(530.81-625.71)	
TTDp	logBM=0.219++2.577logTTDp	170.50	4	−	−	400.62	6	536.58	32	586.70	8
		(155.93-185.06)				(312.36-488.68)		(513.18-559.98)		(558.05-615.35)	
TTDd	logBM=0.461+2.584logTTDd	334.94	2	−	−	452.19	5	540.94	38	624.73	9
		(241.77-428.12)				(353.44-550.93)		(516.22-565.66)		(551.11-698.36)	
Arithmetic Mean		397.88		406.37		435.74		503.86		525.05	
		(320.68-475.08)		(289.50-523.23)		(357.59-513.90)		(456.89-550.83)		(468.12-581.97)	
Weighted Average		402.34		423.34		453.326		520.83		512.40	

Tab. 2 - BM predictions (in g) for the populations of *Prolagus figaro* and *P. sardus* analyzed in this paper. Last two rows, highlighted in gray, show the arithmetic mean of BM calculated for each site, and their weighted average.

HAPDp: proximal humeral anteroposterior diameter; HL: humerus length; HTDd: distal humeral transversal diameter; Lp3: length of the third premolar; N: sample size; SSN: Soprintendenza dei Beni Archeologici per le Provincie di Sassari e Nuoro, sede di Nuoro; TAPDp: proximal tibia anteroposterior diameter; TL: tibia length; TTDd: distal tibia transversal diameter; TTDp: proximal tibia transversal diameter; $\bar{x}$: arithmetic mean; $\bar{x}_w$: weighted mean.

MATERIAL

The samples of *P. figaro* and *P. sardus* come from the Monte Tuttavista karstic complex (E Sardinia; Abbazzi et al. 2004) (Tab. 1). Remains of *P. figaro* come from infillings X3, IVm and X4, pertaining to the Capo Figari/Orosei 1 subcomplex of the *Nesogoral* FC-Orosei 2 subcomplex of the *Microtus* (*Tyrrhenicola*) FC (latest Pliocene/earliest Pleistocene to the late Early Pleistocene; Palombo 2009b). In this context, notice that Palombo (2009b) gave a different relative temporal arrangement of the aforementioned infillings (IVm-X4-X3). Remains of *P. sardus* have been sampled from infillings XIr and VI6, included in the Dragonara subcomplex of the *Microtus* (*Tyrrhenicola*) FC (Middle and Late Pleistocene; Palombo 2009b). Infillings XIr and VI6 were accumulated in a quite short time and their palaeontological contents are taxonomically homogeneous (see Angelone et al. 2008 for discussion). Preliminary analysis of *Prolagus* remains and literature data based on other taxa (Angelone et al. 2009; Palombo 2009b and references therein) pointed out that X3, IVm and X4 also are taxonomically homogeneous infillings. The fossil material is curated at the SSN.

METHODS

The skeletal maturation indicates the complete cessation of longitudinal growth and, consequently, the moment when animals achieve the final BS which is maintained until their death (Peters 1983). Thus, BM estimations of *Prolagus* species were only carried out on individuals that have already attained skeletal maturity (fused epiphyses). Specimens with unfused or broken epiphyses were not considered. *Ochotona*, the extant relative of *Prolagus*, shows a minimal sexual dimorphism (Smith 1988; Nowak 1999). For this reason, we did not assume BM differences between sexes in our fossil sample.

For undertaking the BM estimations, we followed the methodology described and illustrated by Moncunill-Solé et al. (2015: fig. 1). The following measurements were taken on postcranial remains: 1) FL, FTDd and FTDp on femora; 2) HL, HAPDp, HAPDd and HTDd on humeri; and 3) TL, TAPDp, TTDp and TTDd on tibiae. Moncunill-Solé et al. (2015) observed that burrower species of *Ochotona* and leporids show significant differences in the allometric models of the humerus, but not in other skeletal elements (femur and tibia). Although *Ochotona* is the closest relative of *Prolagus*, we preferred to use a general regression model for humeri (i.e. models that include data of leporids and *Ochotona*) because the locomotion of the species of *Prolagus* is not well known. The equations are shown

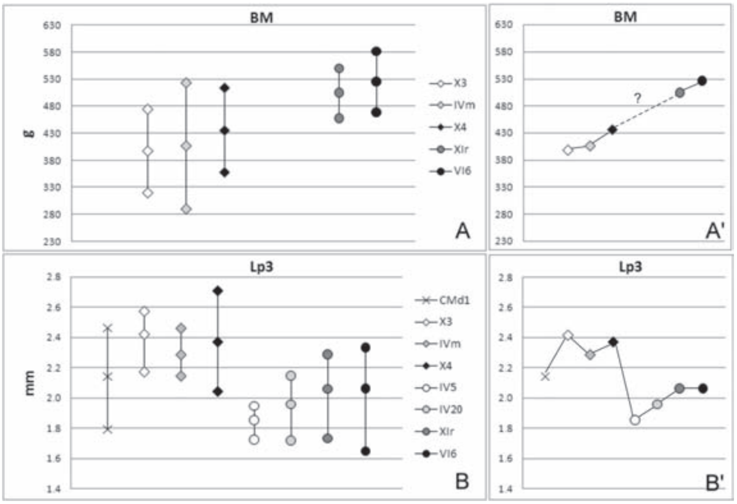

Fig. 2 - BM range A) and Lp3 range B) showing max, average and min values of *Prolagus* aff. *figaro* (cross, CMd1), *P. figaro* (diamonds, X3, IVm, X4) and *P. sardus* (circles, IV5, IV20, XIr, VI6), with detail of average values and trends of BM (A') and Lp3 (B').

in Tab. 2. Once the regression models were applied, we eliminated outliers due to their potential for skewing the distributions. We followed the criterion of Tukey (1977): outliers (Y) were considered when $Y < (Q1-1.5IQR)$ or $Y > (Q3+1.5IQR)$ (where Q1 is the 25th percentile, Q3 is the 75th percentile, and IQR the interquartile range (Q3−Q1)) (Quinn & Keough 2002). For each specific measurement, it was calculated an arithmetic mean ($\bar{x}$) and a confidence interval (IC) [$\bar{x}\pm((\sigma/\sqrt{N})Z_{\alpha}/2)$]. Based on the BM of each measurement, we performed an arithmetic average ($\bar{x}$) and a weighted average ($\bar{x}_W$) [$(X_1W_1+X_2W_2+\ldots+X_NW_N)/(W_1+W_2+\ldots+W_N)$].

In order to compare the different populations of *Prolagus* and analyze the BM variation, we performed ANOVA analyses and post hoc tests (Tukey HSD) ($\alpha = 0.05$) using the IBM SPSS Statistics 19 software.

Results

The results of BM estimations (means, IC, N) are shown in Tab. 2 and are represented in Fig. 1.

For *P. figaro*, we estimate a weight of 397.88 g (320.68-475.08) in fissure filling X3, of 406.37 g (289.50-523.23) in IVm and of 435.74 g (357.59-513.90) in X4. For *P. sardus* the results are greater, 503.86 g (456.89-550.83) in fissure filling XIr and 525.05 g (468.12-581.97) in VI6. We do not observe significant differences between $\bar{x}$ and $\bar{x}_W$ (their difference is ca 10-20 g) and the latter falls perfectly in the IC of the former (Tab. 2). Statistically, there are only significant differences ($p < 0.05$) between the oldest population of *P. figaro* (X3) and the youngest of *P. sardus* (VI6).

When the BM estimations of each measurement are assessed, a similar pattern could be observed comparing the populations with the largest N (VI6 and XIr) (Fig. 1). The variables FTDp and HAPDp estimate a BM far above the arithmetic mean (between 100-200 g greater), especially in VI6 population. The other variables fall next or inside the IC of the arithmetic mean (specially FL, TAPDp, TTDp, TTDd and HTDd). Analyzing the results of the other populations (X3, IVm and X4), we observe more heterogeneous patterns. This may be consequence of: 1) few measurements taken in postcranial bones (3 in IVm and 5 in X4) and 2) small N (ranging from 1 to 11 individuals in X3). However, in this latter population (X3), it is already evident a large value of BM when HAPDp measurement is used, but not in FTDp.

Discussion

BM of Sardinian *Prolagus*: trends and best estimators. Based on dental morphology, a relative temporal arrangement of the studied fissure has been attempted. Preliminary results suggested the relative chronological arrangement X3-IVm-X4 (from older to younger) of populations of *P. figaro* (Angelone et al. 2009). In the case of populations of *P. sardus*, infilling XIr is older than VI6 on the basis of a morphological cline (Angelone et al. 2008). In view of this and the BM results, the three selected populations of *P. figaro* show a total weight increase of ca 10% from the oldest fissure filling (X3) to the youngest (X4) (see Tab. 2, Fig. 1 and 2A). The BM of the oldest population of *P.*

sardus here analyzed (XIr) is ca 15% greater than the youngest of *P. figaro* (X4). The average BMs of the two populations of *P. sardus* selected for this study show a very slight difference (average BM of VI6 is about 4% larger). Finally, the total increase among the oldest (X3) to the youngest populations (VI6) of Sardinian *Prolagus* is of 32% (statistically significant, $p < 0.05$). Thus, we can affirm that Sardinian *Prolagus* increased its BM (average) throughout the Pleistocene.

The best BM estimator for an extinct species not only depends on the accuracy of the model (statistical values), but also on a subjective judgment of the results of predictions (Reynolds 2002). According to the fissure infilling with highest sample (XIr) (Fig. 1d), hindlimb bones seem to be the better BM estimators for *Prolagus* species (as shown also in Moncunill-Solé et al. 2015), particularly FL, TAPDp, TTDp and TTDd. However, HTDd also gives adjusted estimations. All these measurements predicted BM that fall inside the IC of the arithmetic mean and, consequently, we can consider them good proxies for the estimation of BM in the genus *Prolagus*. However, N must be taken into due account. For example, the BM predicted by FL (N=1) in X3 population is far above the arithmetic mean. It is recommendable to work with the largest sample possible in order to better represent the biological variability of the species and, thus, obtain more realistic values. The measurements regarded as the best BM estimators are surprising for two facts. Firstly, zeugopods (tibiae), which are involved in the locomotion and lifestyle of the animal, normally predict worse the BM of mammals (Scott 1990). Secondly, the lengths of long bones are also considered as less accurate than diameters or perimeters (Scott 1990). However, in the case of lagomorphs, the models that use length or zeugopodial measurements are as reliable (coefficient of determination or average absolute per cent prediction) as those that use other postcranial elements, in contrast to other mammalian orders (see also Moncunill-Solé et al. 2015).

Taking into consideration quantitative results, HAPDp measurement overestimates in all populations the BM in *Prolagus* and could not be considered a reliable proxy. FTDp does not show a clear pattern, being far above in the case of XIr population (those with the largest N), but not in others (X3, IVm, X4, VI6). The BM overestimation observed when HAPDp is used for prediction is indicative that this measurement does not only represent the BM of the species but also other biological attributes, such as locomotion or phylogeny. Samuels & Valkenburgh (2008) described some skeletal specializations of rodents depending on their locomotion style. For example, a broad and robust distal humerus is indicative of fossorial or semifossorial habits. We encourage the scientific community to perform new studies that analyze the locomotion, biomechanics and skeletal proportions of *Prolagus* species in comparison with its extant relatives (*Ochotona* spp.). This will increase the biological knowledge of *Prolagus* and might help us to discard those measures that are correlated with their locomotion or phylogeny for predicting BM.

BM and teeth size: the case of Sardinian *Prolagus.* It is interesting to compare the trends of BM vs Lp3 in the *P. figaro* – *P. sardus* lineage. We take into consideration p3 because it is the most reliable tooth position for specific identification in lagomorphs. As shown in Fig. 2b, average Lp3 increases (ca 13%) when the oldest population of *P. figaro* (X3) is compared to *P.* aff. *figaro* from CMd1 site, the "founder" of the Sardinian lineage. Lp3 of *P. figaro* shows a maximum oscillation of 6% in the considered populations. A drastic drop of Lp3 (almost 30%) is recorded between *P. figaro* (X4) and the oldest studied population of *P. sardus* (IV5). After IV5, Lp3 values of *P. sardus* increase slightly through time (total increase of ca 11% in the studied populations) following an asymptotic pattern (see also Angelone et al. 2008). When we analyzed the BM variation, the first thing that we observe is that its record is more incomplete than for teeth: BM estimations are not available for *P.* aff. *figaro* and older populations of *P. sardus* (Fig. 2a). Moreover, we have to take into due account that BM values have been obtained after complex data treatment, whereas Lp3 are raw data. Nevertheless, it is evident that BM and Lp3 of Sardinian *Prolagus* follow quite different trends. The differences are not so evident among populations of *P. figaro*: average BM increases of ca 10%, whereas average Lp3 fluctuates of ca 6%. Evident discrepancies can be noticed with the appearance of *P. sardus*. Average Lp3 drops of ca 30% between youngest *P. figaro* (X4) and oldest *P. sardus* (IV5). Then, Lp3 average increases through time in *P. sardus* attesting to a value of 2.06 mm (VI6) which is ca 15% smaller than in X4. Lacking data relative to older infillings (IV5 and IV20), we can only state that younger ones (XIr and VI6) show a higher BM average (ca 15-20%) than *P. figaro* (X4). Hypothesizing a dramatic BM decrease between *P. figaro* and *P. sardus* followed by an explosive increase to exceed *P. figaro* BM values is not realistic. The most parsimonious hypothesis is that BM followed a general increase trend through the transition *P. figaro-P. sardus* and throughout the evolution of *P. sardus*, countertrending Lp3 drastic drop observed at the transition *P. figaro* – *P. sardus*.

The fact that p3 dimensional trend shows evident discrepancies with BM pattern inferred through postcranial elements casts doubts about the usage of p3 as a proxy for BM estimation in insular endemic *Prolagus*. Compared to continental species of *Prolagus*, insular endemic species show a noticeable enlargement of the size of p3 vs the size of molariform elements of the lower tooth row (see Angelone 2005: fig. 6 for a qualitative comparison) probably due to a reassessment in jaw mechanics. At any rate, the reliability of teeth as BM proxies has been questioned also in studies that took into consideration a continental species of *Prolagus* as well as a wider selection of fossil lagomorphs case studies (Moncunill-Solé et al. 2015). They prefer models based on postcranial bones, as directly related to weight bearing.

Timing and patterns of BM variations in Sardinian *Prolagus*. Mein (1983) illustrated a biphasic pattern of evolution on islands consisting in a first tachytelic step in which the immigrant species undergoes sudden morpho-dimensional changes corresponding to its entrance to insular selective regimes and a second step in which the taxon undergoes a relatively long bradytelic phase. Millien (2006) further corroborated and "quantified" Mein's rule. According to some authors (Sondaar 1977; Alcover et al. 1981; Lister 1989, 1996), the tachytelic stage is a change in the "evolutionary direction" (sensu Sondaar 1977; e.g. BS shift or low gear locomotion) whereas the bradytelic one is a further continuation of the existing "direction of the change" (ib., e.g. harvesting saving by increase of hypsodonty, changes in dentognathic feeding apparatus, or developing traits for searching fallback resources). Evans et al. (2012) estimated a minimum of 4000 years for small mammals to become giants (ca 16000 generations).

If we apply Mein's model to Sardinian *Prolagus* lineage, the first phase should have taken place during or short after the Early/Late Pliocene boundary (age of the CMd1 fossil assemblage). Indeed, *P.* aff. *figaro* from CMd1 shows very slight morphological modifications due to endemism, evidence of its very recent arrival from mainland (Angelone et al. 2015). The Lp3 of *P.* aff. *figaro* is comparable to the values of populations of continental Italy from MN16 (absence record for MN15; Angelone et al. 2015) and is between 7-13% smaller than *P. figaro*. There is no record of the possible changes of BM occurred in the 1 Ma that separate CMd1 and the oldest populations of *P. figaro* from Monte Tuttavista. We have not enough data to clearly recognize the tachytelic stage of Mein's model in *P.* aff. *figaro-P. figaro* and to verify/quantify the dimensional changes and the time span needed to produce them. The populations of *P. figaro* here analyzed should cover a time span of ca 0.3-0.4 Ma (inferred from Palombo 2009b: fig 2). In this time span, slight weight fluctuations have been observed, which may correspond to the bradytelic phase of Mein's model.

The appearance of *P. sardus* (closely related to *P. figaro* and not an immigrant from mainland; Angelone et al. 2015) occurred during the transition from the Orosei 2 subcomplex to the Dragonara subcomplex (ca 0.8-0.7 Ma; inferred from Palombo 2009b: fig 2). This transition is characterized by the highest species turnover recorded in the Quaternary of Sardinia (Palombo 2009b). Leaving aside the reason of this dramatic change (see next section), it seems to have triggered a new biphasic evolutionary phenomenon which follows Mein's model too. In general the phyletic lineages of Sardinian small mammals underwent outright (geologically speaking), an abrupt and noticeable increase in dental size (Abbazzi et al. 2004). Contrarily *Prolagus*, as stated above, experienced a drastic Lp3 decrease. The absence of data from IV5 and IV20 fissure fillings does not allow us to quantify changes in BM. Teeth size and morphology in early populations of *P. sardus* underwent an evolution comparable to Mein's model first phase. The slight, asymptotic growth of *P. sardus* Lp3 and postcranial measurements (Angelone et al. 2008), that in our data covers the interval between ca 0.6-0.4 Ma (inferred from Palombo 2009b: fig. 2), parallelizes Mein's model second phase. Indeed, Mein's rule focuses on the first stages of colonization of the island, making reference to the biological adaptation of the species to the new selective regimes. However later on, changes can also take place consequence of the variation in the environment. Abiotic changes (climatic, topographic, among others) and variations of biotic traits (e.g. levels of predation, intra- and interspecific competition), both have a significant role to drive evolution (Alcover et al. 1981; Brockhurst et al. 2014). Our data seem to indicate that Mein's model can be applied several times to a taxon during its evolution of an island, if significant ecological changes occur (e.g. climatic changes or variation in levels of selective regimes). The study of other mammalian lineages of the Pleistocene of Sardinia or other islands may provide more case studies to support this hypothesis.

Driving factors in the evolution of Sardinian *Prolagus*: some hypotheses. The sea level low stand at the Early/Late Pliocene transition allowed the migration of *P. sorbinii* from Italian mainland towards Sardinia (Angelone & Kotsakis 2001; Angelone et al. 2015). Insular selective regimes triggered the morpho-dimensional changes in the immigrant that led to *P. figaro*. *Prolagus figaro* survived until the end of the Orosei 2 subcomplex. The appearance of *Prolagus sardus* marks the onset of the Dragonara subcomplex, characterized by a complete turnover in the small mammals' component of Sardinian fauna (except for *Talpa*): the leporid and the glirid *Tyrrhenoglis* did not survive the transition; the insectivore *Nesiotites* and the rodents *Tyrrhenicola* and *Rhagamys*, descendants of taxa already present in the Orosei 2 subcomplex, underwent evident modifications of teeth morphology and a noticeable increase of teeth size probably coupled with a BS increase (Abbazzi et al. 2004); the ochotonid *Prolagus* underwent a decrease of Lp3 but an increase of BM.

The ancestors of the small mammal genera which survived into the Dragonara subcomplex were present and already showed endemic traits since the Orosei 2 subcomplex (i.e. *Tyrrhenicola*) or at least since the Capo Figari/Orosei 1 subcomplex. The competition among small mammal species as driving factor of the turnover between the Orosei 2/Dragonara subcomplexes can be ruled out and the extinction of glirids and of the leporid is not likely to have triggered a competition to occupy its niche in taxa with such a wide range of ecological requirements, and the arrival of *Tyrrhenicola* already occurred earlier. The arrival of the canid *Cynotherium* (once regarded as a specialized *Prolagus* hunter, and recently considered a small-prey hunter, possibly also birds, without evident specialization in *Prolagus* hunting; Malatesta 1970; Lyras et al. 2006, 2010) occurred at the onset of the Orosei 2 subcomplex without triggering any sudden, evident change in small mammals, least of all in *Prolagus*, which increases its BM throughout Pleistocene. This fact apparently contradicts van der Geer et al. (2013) who noticed that the BS increase in insular small mammals that occurs following colonization or first appearance, ceases or is reversed after the arrival of mammalian predators or competitors. Probably the impact of a new predator was not so catastrophic because, contrarily to other islands, several carnivores were already present in Sardinia prior to *Cynotherium* (i.e. *Chasmaporthetes*, *Mustela* and *Pannonictis*; the latter also coexisted with *Cynotherium* for a while). In fact, due to its large area, Sardinia had selective regimes more similar to mainland than other Mediterranean islands. It could support the presence of terrestrial predators and had not a strong resource limitation as small islands (Heaney 1978, 1984). Thus, we can not affirm that the arrival of *Cynotherium sardoum* increased the extrinsic mortality of Sardinian pikas.

The most important cause of the turnover at the onset of the Dragonara subcomplex, and thus the trigger of the transition *P. figaro*-*P. sardus* is likely to be climate change, in particular those related to the mid-Pleistocene Transition. Even after Middle Pleistocene, the evolution of *P. sardus* seem related to climate changes and to consequent specific modifications of the environment. Preliminary data by Boldrini & Palombo (2010) suggested a correlation between limb length and temperature in *P. sardus*. Effects of climate on BS have been highlighted in insular endemic fossil vertebrates of the Mediterranean by van der Geer et al. (2013), according to whom BS fluctuates over time linked to climatic oscillation. Also Millien & Damuth (2004) noticed the influence of geographical climatic gradients and climatic change through time on fossil endemic insular species.

Regarding the extinction of Sardinian *Prolagus*, it probably occurred less than 2000 years ago, in the Roman period, between the arrival of *Rattus rattus* and the present time (Vigne 1982). Authors do not agree on the importance of men's influence (directly by predation and indirectly by introduction of alien predators, competitors, parasites, infectious diseases, modification of the landscape by agricultural activities, among others) to the extinction of *Prolagus*.

Insular endemic lagomorphs and the Island Rule. Radical morpho-dimensional adaptations are observed in insular endemic organisms. In mammals, apart from modifications in dental, cranial and limbs morphology and relative proportions, it is observed a BS trend coined as Island Rule (Foster 1964; Van Valen 1973): in general small-sized mammals considerably increase their size, whereas large-sized mammals show an opposite trend. This ecogeographic rule is also observed in insular endemic fossil mammals. In the Neogene-Quaternary of Mediterranean islands and palaeoislands, insular gigantism and dwarfism have been the subject of several studies and debates (from the pioneer general studies, e.g. Vaufrey 1929; Thaler 1973; Sondaar 1977; Azzaroli 1982; to the most recent reviews, e.g. van der Geer et al. 2010; Lomolino et al. 2013 and references therein).

Lagomorphs are usually considered as small mammals together with rodents and insectivores. Although they have a larger size than the average of the small mammals, this order is far from reaching the size of the great majority of large mammals (e.g. elephants, rhinos, etc.). Their medium or intermediate BM undertakes a key position in ecosystems (Valverde 1964) and compromises their response (adaptation) to island environments (Island Rule). Actually in extant endemic insular leporids the BM trend reported in literature is variable, but mostly directed towards a reduction of the size (Foster 1963, 1964; Lawlor 1982; Palacios & Fernández 1992; Tomida & Otsuka 1993). In the case of ochotonids, no extant species are present on islands and their trend is unknown.

When we deal with insular endemic fossil lagomorphs, it is not easy to determine their actual BM and its relative variation compared to the continental ancestor. This is consequence of two facts: 1) mainly most remains consist in teeth, whose size, at least in lagomorphs, does not directly reflect BM (see above and Moncunill-Solé et al. 2015); and 2) the supposed ancestor is often unknown or wrongly identified (e.g. *P. sardus* from *P. michauxi* and *Gymnesicolagus gelaberti* from *P. crusafonti* in Lomolino et al. 2013 and van der Geer et al. 2013). A reliable BS estimation is available for an insular endemic fossil leporid, *Nuralagus rex* (Pliocene of Menorca, Spain), which BM has been calculated in 8 kg (Moncunill-Solé et al. 2015, who reconsidered the BM estimation of 12 kg by Quintana et al. 2011). Even if not quantifiable, the size increase with respect to its supposed continental ancestor, the relatively small-sized genus *Alilepus*, should have been quite remarkable.

For *Prolagus* species it is not possible to quantify exactly the relative BM increase of insular endemic vs their mainland ancestors. In the case of Sardinian *Prolagus*, this is due to the lack of studies of postcranial remains of *P. sorbinii*, whereas in the case of Apulian *Prolagus*, their continental ancestor is not known yet (Angelone 2007; Angelone & Čermák 2015; Angelone et al. 2015). Nevertheless, we can have a gauge of the BM difference between endemic insular *Prolagus* and continental species taking into consideration the only available BM datum of a continental *Prolagus*, i.e. the BM of *P.* cf. *calpensis* from the Late Pliocene of Spain, estimated in ca 320 g (based on average of femurs and tibiae; Moncunill-Solé et al. 2015). Thus, *P. figaro* from Monte Tuttavista X3 had a noticeably larger BM (ca 25%) than an almost coeval western European mainland *Prolagus*. One among the oldest known populations of *P. apricenicus* (Cava Fina F1; BM = ca 282 g; Moncunill-Solé et al. in press) had a BM ca 13% smaller than *P.* cf. *calpensis*, not because it decreased its size in an insular domain, but probably because the continental ancestor of Apulian *Prolagus* was a pre-Messinian, medium-sized species (see Angelone 2007; Angelone & Čermák 2015). Later populations of *P. apricenicus*, weighing ca 601 g (Moncunill-Solé et al. 2015), almost doubled the BM of *P.* cf. *calpensis*.

The known average BM range of both Sardinian species of *Prolagus* (397.88-525.05 g; a BM of 800 g for Mesolithic *P. sardus* inferred by Sondaar & van der Geer (2000) on a qualitative basis has to be verified) is smaller than the populations of *P. apricenicus*, whose BM range is ca 280-600 g (Moncunill-Solé et al. 2015, in press). The other Apulian species, *P. imperialis*, is traditionally considered gigantic, because it has the largest p3. However, our analyses and results make clear that dental remains do not directly reflect actual BM, and sometimes even countertrend postcranial-based results. Pending a study of postcranial remains of *P. imperialis*, we refrain to make inferences about its BM.

Millien (2011) argued that in smaller islands the evolutionary rate is higher. This possibly explains the explosive BM increase of *P. apricenicus*, confined to a very limited, fragmented area, in contrast to the *P. figaro*-*P. sardus* trend, which lived in a larger island.

In general, the scanty available quantitative data indicate that both fossil leporids and ochotonids follow the small mammal Island Rule pattern. They underwent a BM increase which extent is highly variable, though. This trend is not in line with the variable response observed in extant insular endemic leporids (see above).

BM and life history of insular endemic *Prolagus*. In the last twenty years, several researches have been focused on the life history of insular fossil species, principally addressed to dwarfism (Bromage et al. 2002; Raia et al. 2003; Raia & Meiri 2006; Köhler 2010; Kubo et al. 2011; Marín-Moratalla et al. 2011; Jordana et al. 2012, 2013; van der Geer et al. 2014) although, newly, investigations regarding gigantism have been performed (Moncunill-Solé et al. in press; Orlandi-Oliveras et al. in press). BM scales with several traits of the life history of species such as life span, fecundity, age at maturity, among others (Blueweiss et al. 1978; Peters 1983; Calder 1984). For this reason, at first sight, we could think in predicting some of these life history traits for *P. figaro* and *P. sardus* using the BM results of our analysis. However, Moncunill-Solé et al. (in press) analyzed the histology and BM of one of the Apulian insular endemic species of *Prolagus* (*P. apricenicus*) and suggested that it had a slower life history than expected from its BS. Histologically, the longevity is estimated of at least 7 years for *P. apricenicus* from F1 fissure filling contrasting with the 4.5 years expected from its BS (around 300 g). The selective regimes of insular habitats (low levels of extrinsic mortality and resource limitation) are the most probable triggers of this shift (Palkovacs 2003). This is also observed in extant ochotonids (*Ochotona* spp.) that dwell in rocky habitats which are subjected to a low average yearly mortality. They show a slower life history (later age at maturity and longer longevity) than the species of *Ochotona* that live in meadows, although both groups do not have steep differences in BM (Smith 1988).

Taking in consideration of the aforementioned, extant and extinct relative species that dwell in habitats with low levels of extrinsic mortality show a slower life history than expected from their BS. In the case of *P. figaro* and *P. sardus* the levels of extrinsic mortality may not be as low as in the case of *P. apricenicus* from Gargano consequence of the presence of predators. However, the ecological selective regimes of Sardinia would not be like the mainland's one. For this reason, the prediction of life history traits and other biological attributes using the estimated BM should be considered with caution. Probably, we would underestimate the values of these traits. The absence of histological data of extant and extinct ochotonids encourages the studies focused on this field in order to improve the biological knowledge of insular and mainland lagomorphs.

Conclusions

BMs were estimated for *P. figaro* from X3 (397.88 g), IVm (406.37 g) and X4 (435.74 g); and for *P. sardus* from XIr (503.86) and VI6 (525.05 g). These results allow us to state a significant increase of BM of the species *Prolagus* from Sardinia throughout the Pleistocene. The best measurements for determining the BM of *Prolagus* are FL, TAPDp, TTDp, TTDd and HTDd. In contrast, HAPDp and FTDp appear to be unreliable proxies. The BM increase opposes to the pattern of the Lp3, which shows a drastic drop at the transition between *P. figaro* and *P. sardus*. This is due to the fact that teeth are not weight-bearing elements, and thus, their use as BM proxies is not recommended. However, when the teeth dimensions are taken into account, the biphasic Mein's model (tachytelic and bradytelic stages) may be observed twice. This cannot be confirmed with BM estimations due to the absence of postcranial elements in some key sites as CMd1 (*P.* aff. *figaro*) and IV5 (oldest known population of *P. sardus*). The entrance of *Cynotherium* and the presence of other species of carnivores during the Pleistocene seem to not have influence on the pattern of adaption to insular ecological regimes of *Prolagus*.

Currently, the absence of ochotonids on islands does not allow us to know the adaptions of this group to insular ecological regimes (Island Rule). In the fossil record, the two species of *Prolagus* studied in our research and one of the two endemic insular Apulian species (*P. apricenicus*) suggest a gigantism pattern for ochotonids. However, this latter species shows a more explosive increase of BM perhaps as a result that it dwelled in a smaller, fragmented area. It is observed in extant and extinct species that the environments with a lower extrinsic mortality can promote a lower life history (e.g. greater longevity than that expected for its BM). Thus, the estimations of life history traits taking into account the BM results of our research should be considered with caution.

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Chapter 8

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

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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.

RÉSUMÉ

Mots clés :
Histoire de la vie
Règle de l'île
Prolagus

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.

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 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).

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*)
P. apricenicus F1	43	11	12
P. apricenicus F8	24	24	17
P. cf. *calpensis*	10	5	6

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 to1000 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 1λ filter (Zeiss AxioScope 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).

	P. apricenicus F1		*P. apricenicus* F8		*P.* cf. *calpensis*	
FL	269.47	$n = 3$	–	–	–	–
($\log BM = -1.11 + 2.229 \log FL$)	(249.26–289.68)					
FTDp	313.84	$n = 11$	658.80	$n = 14$	369.32	$n = 4$
($\log BM = 0.498 + 2.217 \log FTDp$)	(262.45–365.22)		(612.86–704.73)		(312.00–426.64)	
FTDd	235.83	$n = 6$	553.92	$n = 9$	300.51	$n = 1$
($\log BM = 0.318 + 2.481 \log FTDd$)	(216.90–254.76)		(505.49–602.35)			
FAPDd	276.64	$n = 6$	590.26	$n = 10$	403.69	$n = 1$
($\log BM = 0.225 + 2.63 \log FAPDd$)	(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 though 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.

	P. apricenicus F1	*P. apricenicus* F8	*P.* cf. *calpensis*	*O. princeps*		*O. curzoniae*	
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

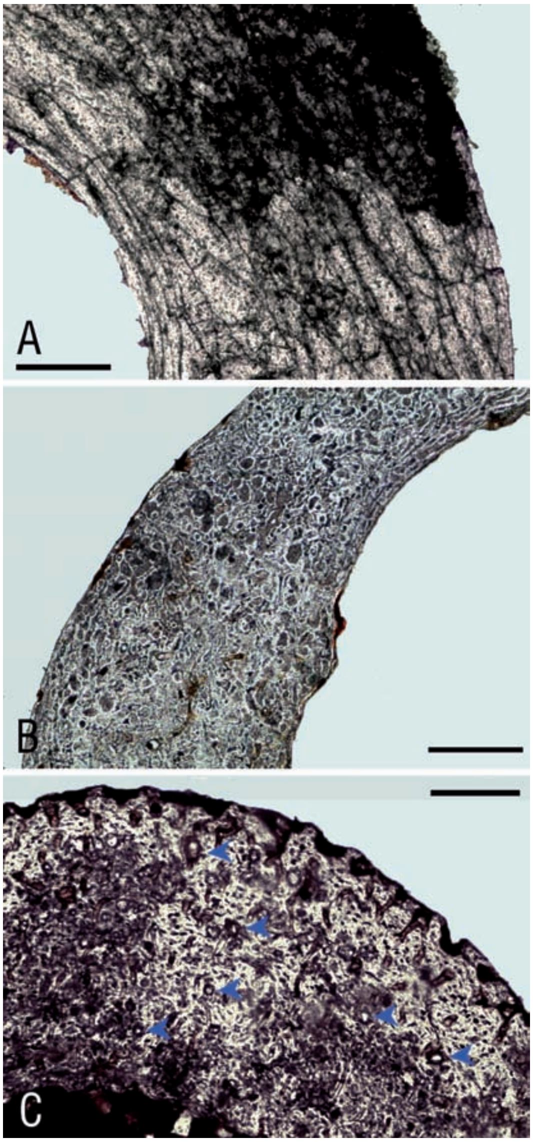

Fig. 1. (Color online.) A. Bone histology of *P.* cf. *calpensis* from Casablanca I (IPS-81937). The bad preservation and microbial attack can be observed. B and C. Bone histology of *P. apricenicus* from Cava Fina F8. B shows the bad preservation (IPS-83559) and C the highly vascularised periosteal 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. apricenicus* de Cava Fina F8. B montre la mauvaise conservation (IPS-83559) et C la forte vascularisation du périoste (IPS-83158). Des ostéones primaires sont indiquées par des pointes de flèche bleues. Échelle : 200 μm (sans filtre).

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 (transverval 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
Prolagus apricenicus 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
Prolagus apricenicus 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
Prolagus cf. *calpensis*			
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

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

3.2.2. *Prolagus apricenicus from Cava Fina F8*

Some of the *P. apricenicus* 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. apricenicus* 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. apricenicus* from

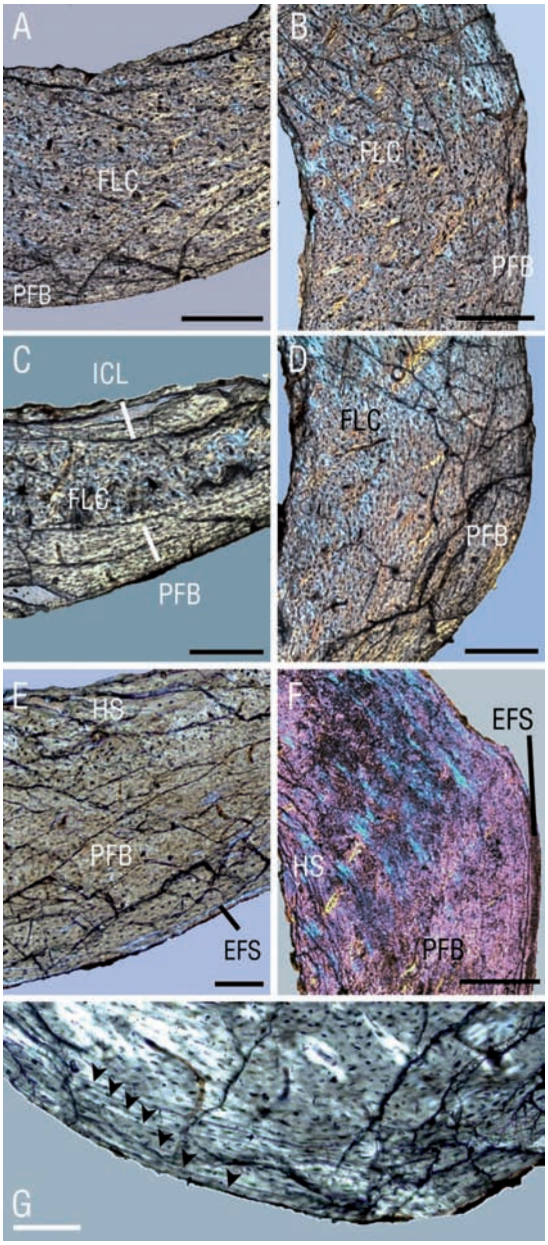

Fig. 2. (Color online.) Bone histology of *P. apricenicus* from Cava Dell'Erba F1 fissure filling. A and B. Anterior and lateral regions of IPS-83892 respectively, a young specimen. It shows the fibrolamellar complex (FLC). C and D. Anterior and lateral regions of IPS-83893 respectively, a mature specimen, 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 1λ 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 1λ) 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 shortail 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

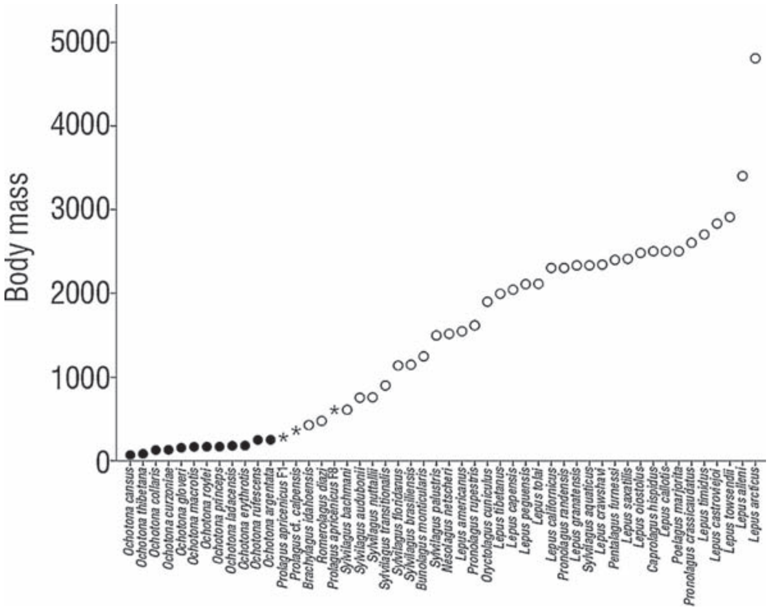

Fig. 3. Representation of the adult body mass (mean) variability of the extant species of lagomorphs and the values obtained in our estimations for *Prolagus* species. Black circles represent the genus *Ochotona*, white circles, leporids, and *Prolagus* species are represented by asterisks. Values for 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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Chapter 9

How common is gigantism in insular fossil shrews? Examining the “Island Rule” in soricids (Mammalia: Soricomorpha) from Mediterranean Islands using new body mass estimation models

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How common is gigantism in insular fossil shrews? Examining the 'Island Rule' in soricids (Mammalia: Soricomorpha) from Mediterranean Islands using new body mass estimation models

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The evolution of organismal body size in extant and extinct ecosystems of islands (Island Rule) is receiving much attention at present. Allometric models are a reliable way to predict the weight of extinct species, but are scarce or even absent for some groups of micromammals. To fill the gap, we carried out regression models with extant species of soricids ($N = 63$) using measurements of teeth, cranium, and postcranial bones, and applied these to fossil insular species and their mainland ancestors. Almost all models are significant ($P < 0.05$), except for those based on the width of occipital condyles. The femur can be considered the most reliable body-mass predictor, producing estimations not far from those derived from teeth (excepting molar widths). Predictions of insular species (in grams) show that those belonging to the tribe Nectogalini [*Asoriculus burgioi* Masini & Sarà, 1998, 27.54; *Asoriculus similis* (Hensel, 1855), 23.68; *Nesiotites ponsi* Reumer, 1979, 14.58; *Nesiotites meloussae* Pons-Moyà & Moyà-Solà, 1980, 24.83; *Nesiotites hidalgo* Bate, 1945, 26–30] had larger masses than *Crocidura* sp. [*Crocidura sicula esuae* (Kotsakis, 1986), 9.50; *Crocidura sicula sicula* (Miller, 1901), 8.60; *Crocidura zimmermanni* Wettstein, 1953, 7–10]. Statistical comparisons with their ancestors revealed that certain species (*Nesiotites* sp. from Mallorca and *A. similis* from Sardinia) may be considered giants, but not *C. zimmermanni* (from Crete). Body size is closely related to life history, which is highly influenced by the selective regimes of the environment. Thus, the lower isolation distance of Crete in comparison with Sardinia and Mallorca, suggesting more introductions of competitors and predators, and the presence of a flow with the mainland, may be the reason for the absence of a giant form of *C. zimmermanni*. However, some biological aspects of species (such as phylogeny or lifestyle) may also have an influential role.

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ADDITIONAL KEYWORDS: body size evolution – body mass estimation – gigantism – Island Rule – Mediterranean Islands – regression models – shrews – Soricidae.

INTRODUCTION

One of the major and significant traits of an organism is its body size, which plays an important role in the biology and ontogeny of species (Calder, 1984), and affects the fitness of individuals (Brown, Marquet & Taper, 1993; Blanckenhorn, 2000). Body size shows tight correlations with physiological and life-history parameters (Peters, 1983; Calder, 1984). It was not until the end of 19th century that body size became the target of investigations. Today, its impact on the ecology of species is well known and intensely studied. For instance, body size controls the degree to which animals contribute to ecosystem nutrient fluxes (Hall *et al.*, 2007), determines the abundance and functional roles in complex food webs (Jacob *et al.*, 2011), marks the threshold for daily

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torpor or hibernation of a species (Geiser, 1998), and influences behavioural traits (Ryan & Brenowitz, 1985). Body size, or its proxy, body mass, is not measurable in fossil remains, and studies testing its importance in extinct ecosystems are not easily carried out (Reynolds, 2002). Traditionally, the tight relationship between body mass and bone dimensions and the statistical methodologies (regression analysis) have allowed researchers to estimate the weights of fossil species (the average body masses) with confidence (Damuth & MacFadden, 1990). Much research has centred on the estimation of body mass in large mammals (primates, elephants, carnivores, or ungulates) (Jungers, 1990; Scott, 1990; Van Valkenburgh, 1990; Christiansen, 2004), whereas weight-predictive models for small mammals are scarce and focused on the order Rodentia (Hopkins, 2008; Millien & Bovy, 2010; Freudenthal & Martín-Suárez, 2013; Moncunill-Solé *et al.*, 2014). For this reason, allometric models for small mammal orders are of the utmost importance to estimate body weight in fossil species and to increase our knowledge of extinct species and their ecosystems, which represent natural habitats unaltered by human intervention.

Rodents, rabbits, and insectivores are coined small mammals or micromammals. Their features (broad distribution, small home ranges, low migration, fast evolution, good preservation, and easy taxonomic identification) make them particularly useful in palaeontology (palaeoenvironmental, palaeoclimatic, biochronological, and taphonomic research; Stoetzel, 2013). Nevertheless, especially in insectivores, their palaeobiology and their palaeo-ecosystems have been less studied (few studies were found that deal with their biology, e.g. body mass estimations or life history). The family Soricidae (true shrews), which is composed of the tiniest living mammals, belongs to this group. Soricids have body masses that range from approximately 1–3 to 80–100 g, depending on the species (Silva & Downing, 1995). Together with talpids (Talpidae family, composed of moles, shrew-moles and desmans), solenodonts (Solenodontidae family, with only two endangered species), and the extinct nesophontids (family Nesophontidae, West Indies shrews), they form the order Soricomorpha, commonly included in the obsolete, non-monophyletic taxon Insectivora.

One of the most interesting issues in the realm of body mass research is the evolution (adaptation) of species that inhabit insular ecosystems, showing impressive shifts in size towards both extremes: dwarfism and gigantism (Island Rule; Foster, 1964; Van Valen, 1973a). In contrast to other orders, insular 'insectivores' do not exhibit any clear tendency of body size towards a dwarf or giant phenotype (Foster, 1964; Lomolino, 1985). The presence of extant and extinct 'insectivores' is documented in islands all over the world (Nowak, 1999). Various Mediterranean Islands are or were inhabited by some soricids (Fig. 1; Table 1), but the scientific community has contradictory opinions about their taxonomy. Several species are known to be currently dwelling on Mediterranean Islands: the endemics *Crocidura sicula sicula* (Miller, 1901) and *Crocidura zimmermanni* Wettstein, 1953, and the species *Crocidura suaveolens* (Pallas, 1811) and *Crocidura russula* (Hermann, 1780) introduced by humans. In extinct Plio–Quaternary faunal complexes, soricid genera are widely identified (Fig. 1; Table 1). The taxonomic controversy of Mediterranean soricids extends into the fossil register. *Nesiotites* is not considered a valid genus by some authors, who instead consider it a large *Asoriculus* (Masini & Sarà, 1998), whereas others take both genera as valid (van der Made, 1999). However, Bate (1944) originally erected the genus *Nesiotites* for the species from the Gymnesic Islands, Sardinia and Corsica. The identification and number of *Crocidura* species have also been matters of discussion (Sarà, Lo Valvo & Zanca, 1990; Hutterer, 1991; Sarà & Vitturi, 1996).

This opens a broad field of investigation. Firstly, our research is focused on performing allometric models for estimating the body mass of soricids using skeletal measurements (teeth, skull, and postcranial bones) that can be applied to fossil or extant remains. Hitherto, the only allometric equations for predicting the weight of soricid species were based on dental measurements of several lipotyphlan and non-lipotyphlan insectivores (Legendre, 1989; Bloch, Rose & Gingerich, 1998). Our second aim is to apply these equations to fossil remains. We will analyse certain fossil species of soricids from the Mediterranean Islands, and their ancestors, to shed light on their body mass evolution. The extinct endemic faunas are considered key for understanding the mechanisms behind the Island Rule because they are not affected by the presence of humans (Masseti, 2009). Furthermore, these new equations allow in-depth studies of the palaeobiology of extinct soricid species and an improved knowledge of extinct ecosystems. They can also be applied to extant species, enhancing biological research hampered by the difficulties involved in studying living individuals.

MATERIAL AND METHODS

The taxonomy used here follows Wilson & Reeder (2005).

Species database

Body mass regression models

Data on extant soricids were collected from 63 species (Table S1), maximizing the taxonomic diversity

Figure 1. Diagram of Mediterranean Islands showing endemic genera and species of soricids from the Plio–Quaternary to the present: white shrew silhouettes, current species; grey shrew silhouettes, extinct or with presence in the fossil record. From west to east: species of *Nesiotites* (extinct) from the Gymnesic Islands; species of *Asoriculus* (extinct) from the Corso-Sardinian complex; *Asoriculus burgioi* (extinct) from Sicily; *Crocidura sicula sicula* (present in the fossil record and extant) and *Crocidura sicula esuae* (extinct) from the Sicilian–Maltese archipelago; *Crocidura zimmermanni* (present in the fossil record and extant) from Crete; and *Crocidura suaveolens praecypria* (extinct) from Cyprus. See text for references.

Table 1. Extant and extinct (Plio–Quaternary) species of soricids in the Mediterranean Islands

Species	Locality	Chronology
Crocidura suaveolens (Pallas, 1811)*	Several islands	Extant
Crocidura russula (Hermann, 1780)*	Several islands	Extant
Crocidura sicula sicula (Miller, 1901)	Sicilian–Maltese archipelago	Late Pleistocene–Extant
Crocidura zimmermanni Wettstein, 1953	Crete	Early Pleistocene–Extant
Nesiotites ponsi Reumer, 1979	Gymnesic Islands	Late Pliocene
Nesiotites meloussae Pons-Moyà & Moyà-Solà, 1980	Gymnesic Islands	Early Pleistocene
Nesiotites hidalgo Bate, 1945	Gymnesic Islands	Middle Pleistocene–Holocene
Asoriculus aff. *gibberodon* (Petényi, 1864)	Corso-Sardinian complex	Middle Pliocene–Late Pliocene
Asoriculus corsicanus (Bate, 1945)	Corso-Sardinian complex	Late Pliocene–Early Pleistocene
Asoriculus similis (Hensel, 1955)	Corso-Sardinian complex	Early Pleistocene–Holocene
Asoriculus burgioi Masini & Sarà, 1998	Sicily	Late Pliocene
Crocidura sicula esuae (Kotsakis, 1986)	Sicilian–Maltese archipelago	Middle Pleistocene–Late Pleistocene
Crocidura suaveolens praecypria Reumer & Oberli, 1988	Cyprus	Middle Pleistocene–Holocene

*Species introduced by humans.

and minimizing the effects of phylogeny (Mendoza, Janis & Palmqvist, 2006). The body size range covers all size diversity of the Soricidae family from *Sorex minutissimus* Zimmermann, 1780 (1.7 g) to large *Crocidura olivieri odorata* Leconte, 1857 (60 g) (Silva & Downing, 1995), and is appropriate for body mass estimations. The collection belongs to the Hungarian Natural History Museum (NHMUS). For several taxa, some bones were not available and these species were excluded from the analyses.

Fossil data

The species of fossils analysed are presented in Fig. 2 and Table 2. We decided not to analyse the body mass of *Nesiotites rafelinensis* Rofes *et al.*, 2012, the earliest species identified of this genus in the Gymnesic Islands, because of its controversial taxonomy (Rofes *et al.*, 2012; Furió & Pons-Monjo, 2013; Rofes *et al.*, 2013). This fossil sample consists of insular genera and their probable ancestors: *Crocidura kornfeldi* Kormos, 1934 is the ancestor of *Crocidura zimmermanni* (Reumer, 1986), and *Asoriculus gibberodon* (Petényi, 1864) is the ancestor of the *Asoriculus similis* (Hensel, 1855) and *Nesiotites* genera (Kotsakis, 1980; van der Made, 1999;

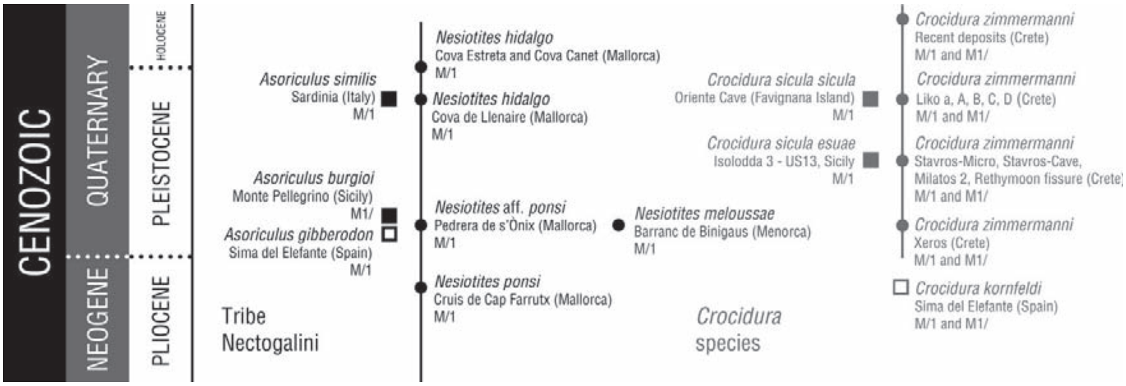

Figure 2. Chronological framework of the species used in the study: in black, species related to the tribe Nectogalini; in grey, *Crocidura* species. The circles highlight the species analysed from different sites sorted biochronologically (connected by a thick line), the squares highlight the species analysed from only one site, and the empty squares highlight the mainland (ancestor) species. Below the species: the site, locality, and molar/s used for estimating body mass are listed.

Table 2. Fossil material used in the present study

Species	Site	Chronology	Bibliography
Asoriculus burgioi	Monte Pelegrino, Sicily	Early Pleistocene	Masini & Sarà (1998)
Asoriculus gibberodon	Sima del Elefante, Spain	Early Pleistocene	Rofes & Cuenca-Bescós (2006)
Asoriculus similis	Sardinia	Late Pleistocene	Rofes *et al.* (2012)
Crocidura kornfeldi	Sima del Elefante, Spain	Late Pliocene	Rofes & Cuenca-Bescós (2011)
Crocidura sicula esuae	Isolidda 3 – US 13, Sicily	Middle Pleistocene	Locatelli (2010)
Crocidura sicula sicula	Oriente Cave, Sicily	Late Pleistocene–Holocene	Locatelli (2010)
Crocidura zimmermanni	Xeros (X), Stavros-Micro (SM), Stavros-Cave (SC), Milatos 2 (M2), Rethymnon fissure (RF), Liko a (La), Liko A (LA), Liko B (LB), Liko C (LC), Liko D (LD), and recent deposits (RD), Crete	Pleistocene–Holocene	Reumer (1986)
Nesiotites ponsi	Cruis de Cap Farrutx (CF), Mallorca	Late Pliocene	Rofes *et al.* (2012)
Nesiotites aff. *ponsi*	Pedrera de s'Ònix (PO), Mallorca	Early Pleistocene	Rofes *et al.* (2012)
Nesiotites meloussae	Barranc de Binigaus (BB), Menorca	Early Pleistocene	Rofes *et al.* (2012)
Nesiotites hidalgo	Cova de Llenaire (CL), Cova Estreta (CE), and Cova de Canet (CC), Mallorca	Late Pleistocene–Holocene	Rofes *et al.* (2012)

Rofes *et al.*, 2012). As the ancestors of *Asoriculus burgioi* Masini & Sarà, 1998 and *Crocidura sicula esuae* (Kotsakis, 1986) – *C. sicula sicula* are not known with reliability (Masini & Sarà, 1998), we decided to compare their body masses with those of the extinct mainland relatives analysed for the other fossil insular species, *A. gibberodon* and *C. kornfeldi*.

MEASUREMENTS

Body mass regression models

Some measurements (in millimetres) of the skull and teeth were taken following Moncunill-Solé *et al.* (2014, 2015): width of occipital condyles, and lower and upper length of the molar tooth row (Fig. 3). Measurements of width and length of the lower and upper M1 were also taken, following the criteria given in Reumer (1984). However, for carrying out the analysis and facilitating the calculations, we simplified his measurements (Reumer described two measurements of width and two of length for each tooth). We described the length of the upper first molar as the average of the BL (buccal length) and LL (lingual length) measurements described by Reumer (1984: fig. 4), width of the upper first molar averaging AW (anterior width) and PW (posterior width), and width of the lower first molar averaging TRW (trigonid width) and TAW (talonid width). The area of the molar (product of length and width of molar) and area of the tooth row (product of molar tooth row length and width of molar) were subsequently calculated. It was noted in rodents that first molar (upper or lower) measurements can over- or underestimate the body mass of some species, depending on the absence or presence of premolars (Freudenthal & Martín-Suárez, 2013). In the case of the Soricidae family, the lower dental formula is constant in all genera investigated here (1P and 3M), but this is not the case for the upper dentition (1–3P and 3M; Hillson, 2005). This will have to be taken into account when estimating the body mass of extinct species. Measurements (in millimetres) of length and the anteroposterior and transversal diameters of the long bone epiphyses (femora, humeri, and tibiae) were also taken (Fig. 3), following the criteria of Moncunill-Solé *et al.* (2014, 2015). Abbreviations are described in Table 3. Rarely, the NHMUS collection recorded the body mass of individuals; thus, data were gathered from the literature (Table S1). Measurements were taken with a digital electronic precision calliper (0.05–mm error).

Fossil data

We compiled data on the dental dimensions (length, width, or tooth row length) reported in the literature (Reumer, 1986; Masini & Sarà, 1998; Locatelli, 2010; Rofes & Cuenca-Bescós, 2006, 2011; Rofes *et al.*, 2012) for the different fossil species cited above (Fig. 2;

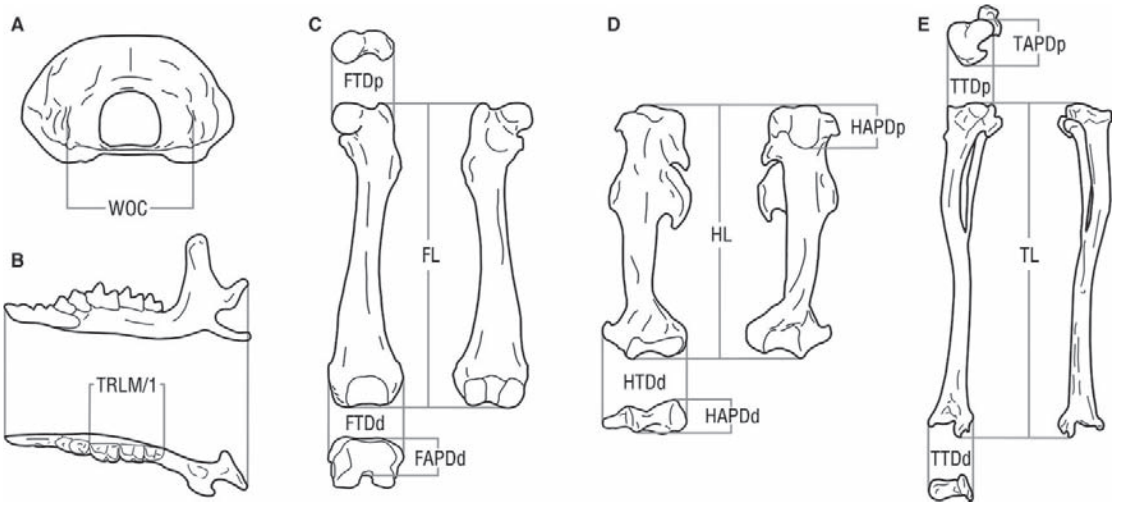

Figure 3. Measurements of mandible, cranium, and postcranial bones. A, cranium: WOC, width of the occipital condyles. B, mandible: TRLM/1, tooth row length of lower molars. C, femur: FL, femur length; FTDp, proximal femoral transversal diameter; FAPDd, distal femoral anteroposterior diameter; FTDd, distal femoral transversal diameter. D, humerus: HL, humerus length; HAPDp, proximal humeral anteroposterior diameter; HAPDd, distal humeral anteroposterior diameter; HTDd, distal humeral transversal diameter. E, tibia: TL, tibia length; TAPDp, proximal tibia anteroposterior diameter; TTDp, proximal tibia transversal diameter; TTDd, distal tibia transversal diameter.

Table 3. Abbreviations of the measurements

Bone	Measurement	Abbreviation	Figure	Bibliography
Teeth	Length of the first lower molar (M/1)	LM/1	–	Reumer (1984)
Teeth	Width of the first lower molar (M/1)	WM/1	–	Reumer (1984)
Teeth	Area of the first lower molar (M/1)	AAM/1	–	Moncunill-Solé *et al.* (2014, 2015)
Teeth	Tooth-row length of lower molars	TRLM/1	2B	Moncunill-Solé *et al.* (2014, 2015)
Teeth	Tooth-row area of lower molars	TRAAM/1	–	Moncunill-Solé *et al.* (2014, 2015)
Teeth	Length of the first upper molar (M1/)	LM1/	–	Reumer (1984)
Teeth	Width of the first upper molar (M1/)	WM1/	–	Reumer (1984)
Teeth	Area of the first upper molar (M1/)	AAM1/	–	Moncunill-Solé *et al.* (2014, 2015)
Teeth	Tooth-row length of upper molars	TRLM1/	–	Moncunill-Solé *et al.* (2014, 2015)
Teeth	Tooth-row area of upper molars	TRAAM1/	–	Moncunill-Solé *et al.* (2014, 2015)
Skull	Width of occipital condyles	WOC	2A	Moncunill-Solé *et al.* (2014, 2015)
Femur	Femur length	FL	2C	Moncunill-Solé *et al.* (2014, 2015)
Femur	Proximal femoral transversal diameter	FTDp	2C	Moncunill-Solé *et al.* (2014, 2015)
Femur	Distal femoral anteroposterior diameter	FAPDd	2C	Moncunill-Solé *et al.* (2014, 2015)
Femur	Distal femoral transversal diameter	FTDd	2C	Moncunill-Solé *et al.* (2014, 2015)
Humerus	Humerus length	HL	2D	Moncunill-Solé *et al.* (2014, 2015)
Humerus	Proximal humeral anteroposterior diameter	HAPDp	2D	Moncunill-Solé *et al.* (2014, 2015)
Humerus	Distal humeral anteroposterior diameter	HAPDd	2D	Moncunill-Solé *et al.* (2014, 2015)
Humerus	Distal humeral transversal diameter	HTDd	2D	Moncunill-Solé *et al.* (2014, 2015)
Tibia	Tibia length	TL	2E	Moncunill-Solé *et al.* (2014, 2015)
Tibia	Proximal tibia anteroposterior diameter	TAPDp	2E	Moncunill-Solé *et al.* (2014, 2015)
Tibia	Proximal tibia transversal diameter	TTDp	2E	Moncunill-Solé *et al.* (2014, 2015)
Tibia	Distal tibia transversal diameter	TTDd	2E	Moncunill-Solé *et al.* (2014, 2015)

Table 2). Teeth were well preserved and easily identified at the species level. Data for individuals were collected, but when they were not available, average values for the species were taken. In these cases, we looked for arithmetic means of measurements with the smallest standard deviation, minimally affecting the body mass estimation of the species.

STATISTICAL MODELS

The allometric model, expressed as the power function $y = ax^b$, was used to estimate the body masses of extinct animals (Damuth & MacFadden, 1990). The power function was log transformed, obtaining a linear relationship ($\log y = \log a + b \log x$) (Peters, 1983). The data were fitted by the method of least squares (OLS, model I), using stepwise methodology for multiple models (Quinn & Keough, 2002). Statistical analyses were performed with SPSS 19 (IBM). The homogeneity of variances was controlled through residuals plots (predicted y versus residuals) and outliers with Cook's distance (D_i). Species with $D_i > 1$ were eliminated and the model was reconstructed again. The precision and adjustment of the allometric models were evaluated by the coefficient of determination, r^2; the standard error of the estimate, SEE ($= \sqrt{\text{residual mean square}}$); and the average absolute percentage prediction, %PE {= [(observed – predicted)/predicted]*100} (Smith, 1980, 1984). Leave-one-out cross-validations (LOOCVs) were undertaken to test the suitability of resultant equations [the cross-validation error is reported as $CVe = \frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2$ where yi is the observed value and $\hat{y}_i$ is the predicted value] (Moncunill-Solé *et al.*, 2014, 2015).

The average of multiple individuals was used to create the models to avoid confusing intra- and interspecific allometry (Moncunill-Solé *et al.*, 2014, 2015). As the sexual size dimorphism is insignificant in small mammals (Lu, Zhou & Liao, 2014), data on males and females were analysed together. However, the specialized skeletal adaptations of postcranial bones reflecting lifestyle and locomotion can bring background noise into the regression models (Moncunill-Solé *et al.*, 2015). For this reason, for each postcranial measurement (femur, humerus, and tibia), we split the different species by groups in relation to locomotion (F, fossorial; P, psammophilic; SA, semiaquatic; SF, semifossorial; SC, scansorial; T, terrestrial) (Table S1; Hutterer, 1985) and regression models were carried out with them. We tested the statistical differences of these equations with an analysis of the covariance (ANCOVA), and we only presented them when the result was significant ($P < 0.05$). We are aware of the large bias towards terrestrial lifestyle, which can cause non-significant results. The model performed with all

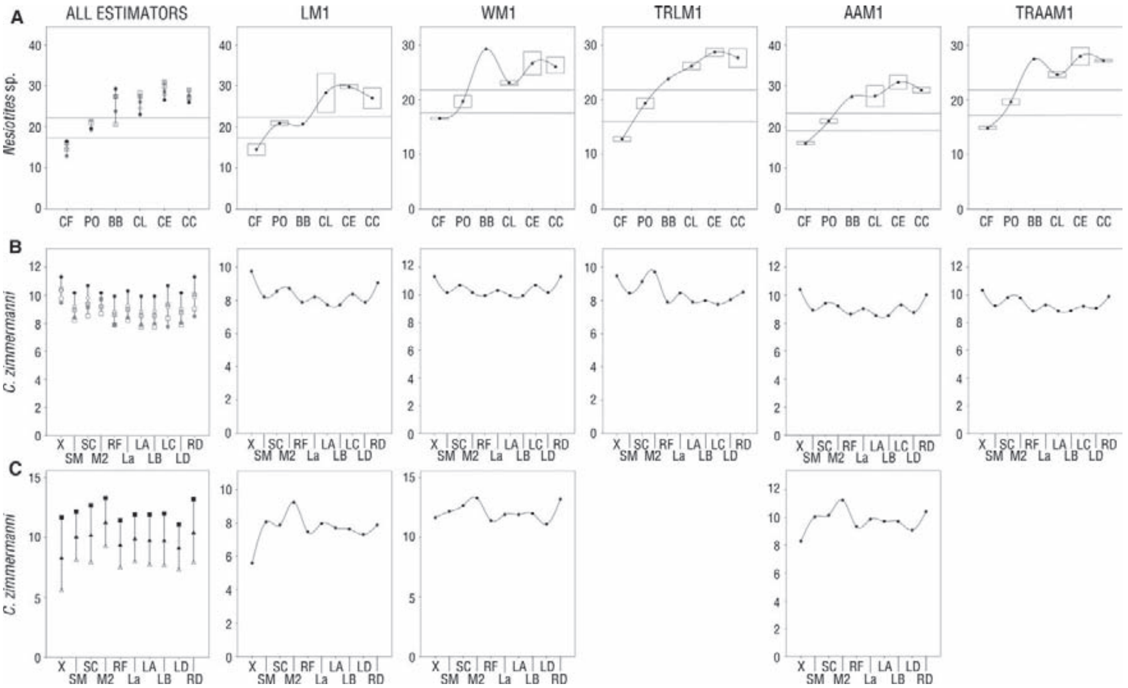

Figure 4. Estimations of body masses (in g) of *Nesiotites* species (row A, lower molars) and *Crocidura zimmermanni* (row B, lower molars; and row C, upper molars) from different sites ordered chronologically (see Table 2 for site acronyms). The first column shows the predictions of body mass using all of the estimators (white square, LM1; black circle, WM1; grey circle, TRLM1; grey square, AAM1; white circle, TRAAM1) and the following columns represent each measurement separately (LM1, WM1, TRLM1, AAM1, and TRAAM1, respectively). In order to observe the fluctuation of the points, we linked the points with a line. Dotted lines in *Nesiotites* diagrams (row A) separate the three statistically different subgroups.

species (A) will always be shown because locomotion habits are likely to be unknown in fossil species.

When body mass estimation models were applied for predicting weights in the fossil register, the results were corrected by a logarithmic correction factor [the detransformed predicted values of each equation (values of body mass) were multiplied by ratio estimation, $RE = \bar{y}/\bar{z}$, where y_i is the observed value of the dependent variable y for the ith observation on the original measurement scale, and z_i is the predicted value for the ith observation, detransformed back to the original measurement scale without correction] (Smith, 1993). For each specific measurement, the average of individuals and the confidence interval (CI) were calculated (Moncunill-Solé *et al.*, 2014). In cases where we worked with arithmetic averages, we decided not to calculate the CI with the standard deviation of the mean because it is not representative of the variation. For the species, the body mass was estimated by simple average ($\bar{x}$) using the different measurements. To test for differences between series of anagenetic species or ancestor and insular species, we performed parametric (Student's t–test and ANOVA) or non-parametric (Mann–Whitney and Kruskal–Wallis) tests, as appropriate for the sample ($P < 0.05$) (Schwartz, Rasmussen & Smith, 1995).

RESULTS

The results of the regression models are shown in Table 4 and Figure S1; results of body mass estimations of fossil species are shown in Table 5 and Fig. 4.

BODY MASS ESTIMATION MODELS

Simple models were carried out for lower and upper M1, providing significant results ($P < 0.05$) for all metric parameters used. The coefficient of determination was around 0.7, with higher scores for the TRL (tooth-row length) of both teeth (0.825 for M/1 and 0.822 for M1/) and lower scores for WM/1

Table 4. Allometric regression models for the estimation of body mass (in g) in the family Soricidae

Measurement	N	a	b	P	r^2	SEE	%PE	RE	CVe	HV	D_i
Lower M1											
LM/1	58	0.291	3.061	0.000	0.736	0.171	33.500	1.078	52.368	✓	✓
WM/1	58	0.967	2.417	0.000	0.660	0.194	37.272	1.112	29.131	✓	✓
TRLM/1	56	–1.248	3.597	0.000	0.825	0.135	25.382	1.038	11.647	✓	✓
AAM/1	58	0.635	1.514	0.000	0.777	0.157	30.213	1.066	18.065	✓	✓
TRAAM/1	56	0.038	1.504	0.000	0.749	0.162	30.294	1.065	15.739	✓	✓
Upper M1											
LM1/	63	0.324	3.218	0.000	0.789	0.154	28.537	1.049	24.201	✓	✓
WM1/	63	0.327	2.611	0.000	0.720	0.178	31.314	1.080	18.965	✓	✓
TRLM1/	62	–1.069	3.730	0.000	0.822	0.143	26.425	1.044	16.487	✓	✓
AAM1/	63	0.298	1.505	0.000	0.784	0.156	28.862	1.053	13.877	✓	✓
TRAAM1/	62	–0.307	1.610	0.000	0.796	0.153	28.191	1.048	15.346	✓	✓
Femur											
FL	29	–1.836	2.883	0.000	0.819	0.155	26.846	1.060	47.690	✓	✓
FTDp	29	0.084	2.757	0.000	0.854	0.140	22.065	1.075	33.063	✓	✓
FAPDd	29	0.497	3.136	0.000	0.853	0.140	23.315	1.055	21.491	✓	✓
FTDd	28	0.075	2.606	0.000	0.833	0.148	25.125	1.087	38.527	✓	✓
Humerus											
HL	28	–1.737	2.963	0.000	0.773	0.170	28.517	1.056	28,301	✓	✓
HAPDp	30	0.468	2.576	0.000	0.829	0.155	28.534	1.054	76.709	✓	✓
HTDd	28	–0.033	2.317	0.000	0.810	0.155	27.826	1.112	74.892	✓	✓
HAPDd	26	0.954	3.409	0.000	0.791	0.161	27.809	1.084	46.847	*Suncus etruscus and Crocidura nana*	✓
HTDd/HL	28	–0.896	1.626/1.263	0.000	0.856	0.137	23.425	1.071	54.369	✓	✓
Tibia											
TL	13	–2.447	2.962	0.000	0.696	0.123	23.605	1.027	80.014	✓	✓
TTDp	15	0.284	2.317	0.000	0.775	0.113	19.130	1.033	71.526	✓	✓
TAPDp	15	0.498	1.823	0.001	0.607	0.149	27.214	1.053	42.674	✓	✓
TTDd	17	0.160	3.097	0.001	0.841	0.112	20.498	1.029	35.618	✓	✓

Measurements (in mm) used in the model (acronyms for measurements are described in Table 3): N, sample; a, constant of the model; b, allometric coefficient of x; P value, significance < 0.05; r^2, coefficient of determination; SEE, standard error of the estimation; %PE, average absolute percentage prediction; RE, ratio estimation; CVe, cross-validation error; HV and D_i (both ticked with homogeneity of variances or $D_i < 1$. The species that do not satisfy these requirements were eliminated from the model).

(0.660). The parameters of accuracy (SEE and %PE) were within an acceptable range but, in some cases, were slightly high (for instance, WM/1), and the cross-validations showed suitability for most of the models. Several multiple models were carried out: with M/1 variables, with M1/ variables, and with variables of both molars. In two models (M/1 and both molars), the stepwise methodology only selected one variable. Conversely, the M1/ multiple model chose two variables (LM1/ and TRLM1/). However, the model was excluded because the homogeneity of variances was not suitable for prediction. A model with WOC variables was also performed. Despite its significant results ($P < 0.05$), it was considered invalid because of the small sample of species ($N = 5$), the low r^2, and the high values of the accuracy parameters (SEE and %PE).

Postcranial bones showed significant simple regressions ($P < 0.05$) for all parameters. The femur had higher coefficients of determination (r^2: 0.819–0.854) and better cross-validations (*CVe* < 47.690) than the other long bones (r^2: 0.607–0.841), but the accuracy was better in tibia models (SEE < 0.123 and %PE < 23.605), with the exception of TAPDp (proximal tibia anteroposterior diameter). Differences among regression models with species data split by their locomotor lifestyle were non-significant ($P > 0.05$ for ANCOVA of all skeletal traits; Table S2). Five multiple models were carried out using the following: (1) femur variables; (2) humerus variables; (3) tibia variables; (4) all postcranial variables (femur, humerus, and tibia); and (5) all skeletal variables (including postcranial, cranial, and teeth parameters). Except for the humerus (second model),

Table 5. Body mass estimations (in g) of extinct soricids: *Asoriculus gibberodon, Asoriculus burgioi*, *Asoriculus similis*, *Crocidura kornfeldi*, *Crocidura sicula esuae*, *Crocidura sicula sicula*, *Crocidura zimmermanni*, and *Nesiotites* species (rows, grouped by upper and lower molar samples)

Lower molars

Species	Locality	LM/1	WM/1	TRLM/1	AAM/1	TRAAM/1	Mean and CI
Asoriculus gibberodon	Sima del Elefante, Spain	8.97 (8.18–9.75)	9.49 (8.57–10.40)	7.98	8.93 (8.16–9.69)	–	8.85 (8.22-9.46)
Asoriculus similis	Sardinia	27.51 (27.16–27.89)	20.35 (19.98–20.71)	23.87 (23.08–24.66)	25.04 (24.98–25.22)	21.62 (21.35–22.44)	23.68 (21.20–26.15)
Crocidura kornfeldi	Sima del Elefante, Spain	7.17 (6.85–7.49)	10.16 (9.89–10.43)	–	8.36 (8.07–8.64)	–	8.56 (4.12–13.00)
Crocidura sicula esuae	Isolidda 3 – US 13, Sicily	7.13 (6.94–7.31)	12.18 (11.85–12.51)	9.21 (8.76–9.66)	9.18 (8.92–9.45)	10.05 (8.95–11.16)	9.55 (7.95–11.15)
Crocidura sicula sicula	Oriente Cave, Favignana Island	6.14 (5.63–6.64)	10.71 (10.17–11.24)	8.47 (7.64–9.29)	8.04 (7.64–8.44)	9.89 (9.16–10.62)	8.65 (7.10–10.20)
Crocidura zimmermanni	Xeros, Crete	9.76	11.33*	9.47	10.12	10.33	9.92 (9.54–10.30)
Crocidura zimmermanni	Stavros–Micro, Crete	8.22	10.18*	8.43	8.95	9.21	8.70 (8.25–9.15)
Crocidura zimmermanni	Stavros–Cave, Crete	8.55	10.68*	9.14	9.40	9.82	9.23 (8.71–9.75)
Crocidura zimmermanni	Milatos 2, Crete	8.71	10.18*	9.72	9.21	9.77	9.35 (8.86–9.84)
Crocidura zimmermanni	Rethymnon fissure, Crete	7.90	9.94*	7.91	8.64	8.83	8.32 (7.84–8.80)
Crocidura zimmermanni	Liko (a, A, B, C, D), Crete	8.21, 7.74, 7.74, 8.38, 7.89	10.30*, 9.94*, 9.94*, 10.68*, 10.18*	8.43, 7.91, 7.98, 7.76, 8.06	9.02, 8.56, 8.56, 9.31, 8.78	9.28, 8.83, 8.86, 9.17, 9.04	8.74 (8.25–9.22), 8.26 (7.75–8.77), 8.29 (7.78–8.79), 8.66 (7.95–9.36), 8.44 (7.90–8.99)
Crocidura zimmermanni	Recent deposits, Crete	9.05	11.33*	8.51	10.04	9.88	9.37 (8.67–10.07)
Nesiotites ponsi	Cruis de Cap Farrutx, Mallorca	14.53 (13.11–15.94)	16.59 (16.39–16,79)*	12.82 (12.41–13.23)	16.10 (15.75–16.46)	14.86 (14.58–15.13)	14.57 (13.25–15.90)
Nesiotites aff. *ponsi*	Pedrera de s'Onix, Mallorca	20.96 (20.41–21.50)	19.66 (18.58–20.76)*	19.32 (18.37–20.26)	21.46 (20.96–21.96)	19.60 (19.08–20.12)	20.34 (19.32–21.35)

Table 5. *Continued*

Lower molars

Species	Locality	LM/1	WM/1	TRLM/1	AAM/1	TRAAM/1	Mean and CI
Nesiotites meloussae	Barranc de Binigaus, Menorca	20.71	29.27*	23.79	27.39	27.41	24.83 (21.66–27.99)
Nesiotites hidalgo	Cova de Llenaire, Menorca	28.32 (23.60–33.03)	23.04 (22.65–23.43)*	26.12 (25.45–26.80)	27.51 (24.95–30.07)	24.57 (24.04–25.09)	26.63 (25.01–28.24)
Nesiotites hidalgo	Cova Estreta, Menorca	29.82 (29.32–30.32)	26.61 (24.49–28.73)*	28.62 (27.87–29.37)	30.89 (29.23–32.56)	27.91 (26.26–29.55)	29.31 (28.02–30.60)
Nesiotites hidalgo	Cova de Canet, Menorca	27.01 (24.50–29.52)	26.02 (24.80–27.24)*	27.61 (25.86–29.35)	28.98 (28.32–29.64)	27.09 (26.90–27.28)	27.67 (26.78–28.57)

Upper molars

Species	Locality	LM1/	WM1/	TRLM1/	AAM1/	TRAAM1/	Arithmetic mean
Asoriculus burgioi	Monte Pellegrino, Sicily	30.50	24.30	–	27.82	–	27.54 (24.02–31.06)
Crocidura kornfeldi	Sima del Elefante, Spain	6.55 (5.89–7.06)	10.85 (10.13–11.40)	–	8.51 (1.84–9.03)	–	8.64 (6.20–11.07)
Crocidura zimmermanni	Xeros, Crete	5.61	11.67*	–	8.25	–	6.93 (4.34–9.52)
Crocidura zimmermanni	Stavros–Micro, Crete	8.07	12.17*	–	10.02	–	9.05 (7.13–10.96)
Crocidura zimmermanni	Stavros–Cave, Crete	7.90	12.68*	–	10.16	–	10.03 (5.86–14.20)
Crocidura zimmermanni	Milatos 2, Crete	9.25	13.29*	–	11.24	–	10.25 (8.30–12.20)
Crocidura zimmermanni	Rethymnon fissure, Crete	7.47	11.42*	–	9.33	–	8.4 (6.58–10.22)
Crocidura zimmermanni	Liko (a, A, B, C, D), Crete	7.98, 7.72, 7.64, –, 7.31	11.92*, 11.92*, 12.00*, –, 11.11*	–	9.85, 9.71, 9.70, –, 9.08	–	8.92 (7.08–10.75), 8.72 (6.76–10.67), 8.67 (6.65–10.69), –, 8.20 (6.46–9.93)
Crocidura zimmermanni	Recent deposits, Crete	7.89	13.20*	–	10.40	–	9.15 (6.69–11.60)

AAM1, area of first molar; LM1, length of first molar; TRAAM1, tooth-row area of molars; TRLM1, tooth-row length of molars; WM1, width of first molar.
*Not used for calculating the arithmetic mean (see section "Body mass estimation in fossils").

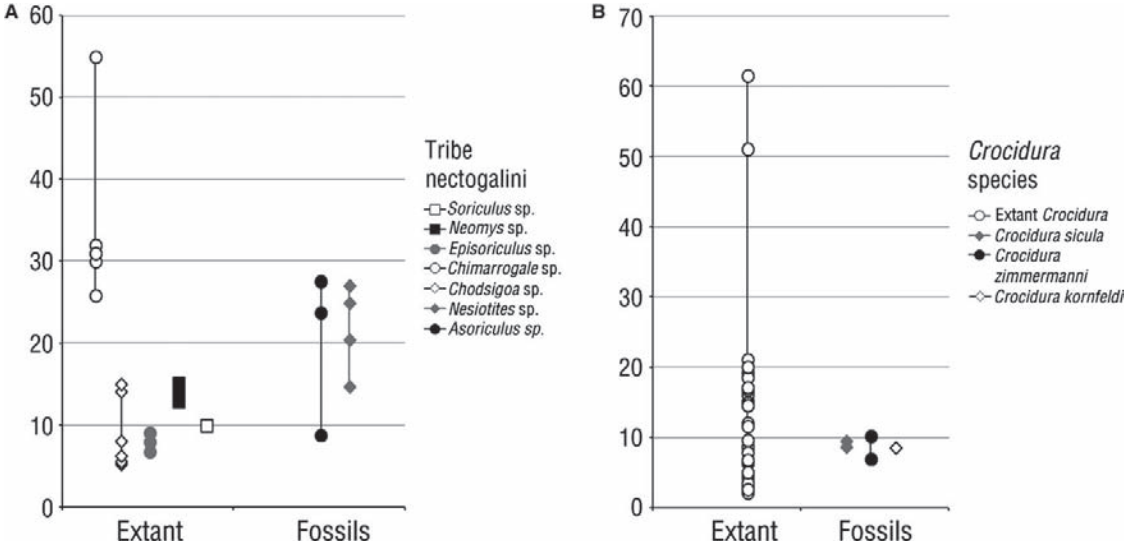

Figure 5. Diagrams comparing the body mass (in g) of extant relatives and fossil species: A, extinct *Asoriculus* and *Nesiotites* species and the extant species of the tribe Nectogalini; B, extinct and extant *Crocidura* species. Lines indicate the body mass range of groups. See the legend for symbols.

the stepwise methodology only selected one variable (model 1, FAPDd; model 3, TTDd; model 4, HTDd; and model 5, TTDd). The multiple humerus model (HTDd and HL) was significant, with a higher coefficient of determination ($r^2 = 0.856$) and accuracy, and lower SEE and %PE, than bivariate regressions.

Body mass estimation in fossils

The insular species Asoriculus (A. burgioi and A. similis) and Nesitoties

The body mass of *A. burgioi* was estimated from measurements of the upper first molar of the holotype with a result of 27.54 g (Table 5) and, in the case of *A. similis*, from the lower first molar, obtaining a mean of 23.68 g (Table 5).

On the other hand, body masses of different anagenetic species of *Nesiotites* were predicted using lower first molars (Fig. 2). Body mass estimations for *Nesiotites ponsi* Reumer, 1979 ranged from 12.82 to 16.59 g, for *Nesiotites* aff. *ponsi* ranged from 19.32 to 21.46 g; for *Nesiotites meloussae* Pons-Moyà & Moyà-Solà, 1980 ranged from 20.71 to 29.27 g, and for *Nesiotites hidalgo* Bate, 1945, from three different sites, ranged from 23.04 to 30.89 g (Table 5). The width of the lower first molar (WM/1) was the dental trait that showed the highest variation in predictions, estimating the largest body masses for some species (*N. ponsi* and *N. meloussae*), but the lowest for others (*N. hidalgo* from the three different sites), in contrast to the other measurements (Fig. 4A). Therefore, in addition to the low suitability and reliability of the regression model (see below), we decided to exclude the body mass estimations performed with WM/1 to calculate the average body mass. The weights of the following taxa were estimated as: *N. ponsi*, 14.58 g; *N.* aff. *ponsi*, 20.34 g; *N. meloussae*, 24.83 g; *N. hidalgo* from Cova de Llenaire, 26.63 g, from Cova Estreta, 29.31 g, and from Cova de Canet, 27.67 g (Fig. 4A; Table 5). Significant differences among groups were observed ($P < 0.05$), identifying three different subgroups: (1) *N. ponsi*; (2) *N.* aff. *ponsi*; and (3) *N. meloussae–N. hidalgo* (from the three sites) (Fig. 4).

Insular species of Crocidura (C. sicula esuae, C. sicula sicula, and C. zimmermanni)

Lower first molar measurements were used to estimate the body masses of subspecies of *C. sicula*. *Crocidura sicula esuae* was predicted to weigh around 9.5 g and *C. sicula sicula* was predicted to weigh 8.6 g (Table 5). The two fossil species belong to sites of different islands (Sicily and Favignana Island, respectively), but during some time in the Pleistocene, it is known that Sicily, Malta, and Egadi Islands formed a single island (Hutterer, 1991). As the connection and disconnection process is not known with certainty, we decided not to test whether these anagenetic species showed significant differences because island area may influence body size evolution (Heaney, 1978; Lomolino *et al.*, 2012).

The body mass of *C. zimmermanni* was estimated from six fossiliferous sites and from one recent deposit with measurements of the upper and lower first molar (Fig. 2). Analysing the lower molars, the body mass estimations were similar for all of the sites, ranging from somewhat larger values in Xeros (11.33 g, WM/1), Stavros-Cave (10.68 g, WM/1), or recent deposits (11.33 g, WM/1), to lower estimations for Liko A, B (7.74 g at both sites, LM/1), and C (7.76 g, TRLM/1). In general, the estimations derived from WM/1 were two points beyond the rest of the parameters. WM/1 showed a weaker relationship with body mass (see below) and, as a result, we decided to exclude it when the arithmetic averages were calculated (Table 5). The different sites did not show significant differences ($P > 0.05$), except for Xeros [$P < 0.05$ with LA (Liko A), LB (Liko B), LD (Liko D), and RF (Rethymnon fissure)] (Fig. 4B). Examining the weight estimations performed with the upper molars, we observed that WM1/ showed the highest estimations, as in the case of lower molars. We also decided to exclude their values for the calculation of the arithmetic mean for the same reasons as mentioned previously. The body mass of *C. zimmermanni* was around 6.93–10.25 g. The several sites did not present significant differences ($P > 0.05$), excepting Xeros, which differed from four other sites (as in M/1) (Fig. 4C).

The weights estimated from upper and lower first molars were similar, ranging from 8.26 to 9.92 g and from 6.93 to 10.25 g, respectively, without significant differences ($P > 0.05$; Table 5).

Mainland species (A. gibberodon and C. kornfeldi)

We estimated the weight of *C. konfeldi* using upper and lower molars, whereas for *A. gibberodon* we only used the lower molar. We predicted a weight of approximately 8.5 g for *C. kornfeldi*, without significant differences between lower and upper molars ($P > 0.05$), and a weight of approximately 8.85 g for *A. gibberodon* (Table 5). With regards to *Crocidura*, the differences between the weights of *C. kornfeldi*, *C. sicula esuae*, *C. sicula sicula*, and *C. zimmermanni* were not significant ($P > 0.05$). Nevertheless, when the differences between *Asoriculus–Nesiotites* species were tested, different subgroups were identified ($P < 0.05$): (1) *A. gibberodon*; (2) *N. ponsi*; (3) *N.* aff. *ponsi–A. similis–N. meloussae*; and (4) *N. hidalgo–A. burgioi*. Statistically, insular species of *Asoriculus* and *Nesiotites* were larger than the mainland species.

DISCUSSION

Body mass estimation models

Teeth and postcranial bones are two types of remains that palaeontologists use for reconstructing the body mass of extinct species (Damuth & MacFadden, 1990). Historically, tooth measurements are most often used as a result of their easy taxonomic determination and prevalence in the fossil record (Legendre & Roth, 1988; Hopkins, 2008). Even so, postcranial limb bones are directly involved in weight-bearing (Janis, 1990), and provide a closer allometric relationship and better results (Scott, 1990; Köhler, 1993; Egi, 2001; Mendoza *et al.*, 2006). This pattern was observed in several mammalian orders, from ungulates to rodents (Scott, 1990; Köhler, 1993; Millien & Bovy, 2010; Moncunill-Solé *et al.*, 2014, 2015). Nevertheless, the allometric models obtained for soricids do not suggest this pattern. Firstly, all models obtained for predicting the body masses of soricid species are significant ($P < 0.05$), but with weaker results than in other micromammal orders (r^2: 0.607–0.854; %PE: 19.130–37.272) (Reynolds, 2002; Hopkins, 2008; Millien & Bovy, 2010; Moncunill-Solé *et al.*, 2014, 2015). The tinier dimensions of soricids (measurements and body mass) and the associated error (the error is proportionally greater in small measures; Senar, 1999) have significantly contributed to the lower values. In this case, teeth models do not show much lower coefficients of determination and higher %PE and SEE than postcranial measurements, as expected. All femoral metric traits show coefficients of determination above 0.8 and low SEE and %PE values, becoming the most satisfactory models (Reynolds, 2002; Moncunill-Solé *et al.*, 2014, 2015). Considering r^2, the models performed with tibiae are less reliable than those calculated with the femur and humerus, but the associated error (SEE and %PE) seems to be lower. Generally, zeugopods (tibia, fibula, radius, and ulna) are worse body mass estimators because of their morphological adaptations related to habitat preference and mode of locomotion (Damuth & MacFadden, 1990; Mendoza *et al.*, 2006). Thus, we do not recommend the use of tibiae as a single body mass predictor but as a supplement to other estimations. The parameters of the femur can be considered the best proxies for reconstructing the body mass of soricids.

The allometric models that were carried out with species grouped by locomotion were not statistically different. This may be consequence of the large number of terrestrial species in front of species of other lifestyles, as discussed above (Table S1; Hutterer, 1985). In studies where locomotor adaptations are significant for describing allometric models, the number of species for each lifestyle is substantially higher (Moncunill-Solé *et al.*, 2015).

In micromammals, teeth are the remains habitually used for identifying the species because, for the moment, postcranial elements have been studied rarely (Angelone, 2005; Furió & Santos-Cubedo, 2009; Weissbrod, 2013). As the reliability of allometrical models of teeth and postcranial elements is very similar in soricids (Table 4), we considered the use of molar measurements optimal for estimating the body mass of extinct soricid species because these dimensions are more often reported in the literature (Fortelius, 1990).

Estimating the weight of fossil soricids

This study is the first to offer specific regression models for estimating the body mass of Soricidae species. We decided to test them against the fossil register, and the weight of certain species was predicted for the first time (*A. burgioi*, 27.54 g; *A. similis*, 20.35 g; *C. sicula esuae*, 9.5 g; *C. sicula sicula*, 8.6 g; Table 5). The body masses of *A. gibberodon*, *C. kornfeldi*, *C. zimmermanni*, and species of *Nesiotites* were estimated previously (Lomolino *et al.*, 2013; Van der Geer *et al.*, 2013). Some of their results differ from our estimates (around 11–15 g for *C. zimmermanni* from the different sites, 35–45 g for *N. hidalgo*, 36.2 g for *N.* aff. *ponsi*, and 21.5 g for *N. ponsi*), but not all of them (9.28 g for *A. gibberodon*; 11.4 g for *C. kornfeldi*). These authors implemented general allometric models (Bloch *et al.*, 1998), including several 'insectivore' species (Soricidae, Talpidae, Erinaceidae, Mascroscelididae, and Tupaiidae) that show different dental formulae (Hillson, 2005). The data set of extant species is critical for body mass predictions, providing better results when taxonomically close species are chosen (Damuth, 1990; Millien & Bovy, 2010). Unique dental formulae imply different relationships between body mass and teeth dimensions, causing less reliable body mass predictions (Janis, 1990). Hence, our regression models that are exclusively based on extant soricids define the relationship among teeth variables and body mass for the family Soricidae better, and the weight predictions of fossil species will be more accurate and reliable.

Assessing the results, we observed that molar widths (WM/1 and WM1/) predicted body masses that were far away from the trend of the other measurements (Schwartz *et al.*, 1995; Millien & Bovy, 2010). This might have been consequence of width being greatly influenced by orientation when measuring. Erratic values for width are especially perceptible in species assessed from different sites (*C. zimmermanni* and species of *Nesiotites*; Fig. 4), and are in line with the statistical results of regression models (Table 4). In these cases we decided to exclude the width results when an arithmetic mean was calculated, but not for species assessed from a single site, because we did not know the allometric relationship in those particular cases. Hence, we encourage the use of other variables instead of molar width for weight predictions in soricids (this trend was also observed in other mammalian groups, see Damuth, 1990; Fortelius, 1990; Janis, 1990; Schwartz *et al.*, 1995).

In two species of *Crocidura* (*C. kornfeldi* and *C. zimmermanni*), predictions were performed with upper and lower first molars without significant differences found among them, as has been observed in other orders of mammals (Janis, 1990; Schwartz *et al.*, 1995). The variation in the number of premolars in the upper dentition among species does not seem to under- or overestimate the body mass, as is observed in some families of rodents (Freudenthal & Martín-Suárez, 2013). This confirms the similar statistical results of their regression models (Table 4), and we promote the use of both first molars for predicting the body mass of extinct species.

The body masses of *Nesiotites* and *Asoriculus* species (insular and mainland) were contextualized with the weight of their extant relatives (tribe Nectogalini) (Fig. 5A; Silva & Downing, 1995). The fossil species are heavier than the extant genera, excepting *Chimarrogale* Anderson, 1877 (aquatic and semi-aquatic shrews distributed throughout the Oriental region). Fossil *Crocidura* species fall within the normal body mass range of their current representatives (Fig. 5B; Table S1), between 2 and 20 g, excepting *Crocidura flavescens* (Geoffroy, 1827) and *C. olivieri odorata* (Silva & Downing, 1995). Insular *Asoriculus* and *Nesiotites* species showed significant differences with their ancestor (*A. gibberodon*), but this is not the case for *Crocidura* species (Table 5). In the light of these results, we consider the *Asoriculus* and *Nesiotites* species as genuine insular giants, but not the *Crocidura* species.

The island rule and the soricid family

The evolution of body size, and specifically the pattern commonly called the Island Rule, is extensively studied in extant faunas (Heaney, 1978; Lomolino, 2005; Lomolino *et al.*, 2012), but is less studied in the fossil register owing to the complexity of estimating size (or mass) (Sondaar, 1977; Palombo, 2009). Recently, Lomolino *et al.* (2013) and Van der Geer *et al.* (2013) have published some aspects of body size changes in island forms. Lomolino *et al.* (2013) noted that palaeo-insular mammals have a more pronounced gigantism and dwarfism than extant faunas. Van der Geer *et al.* (2013) tested the influence of ecological interactions on temporal trends and concluded that small mammals evolved towards larger sizes when no mammalian competitors or predators were present, but that this trend was less pronounced or was reversed when there were colonizations from the mainland. Some results of this latter research conflict with our findings. We have observed that weight in *C. zimmermanni* is actually constant without significant differences among sites (excepting X (Xeros) with LA, LB, LD, and RF) (Fig. 4B, C; for their results, see Van der Geer *et al.*, 2013: tables S6 and S13), and that populations of *N. hidalgo* do not show statistical differences (for their results, see Van der Geer *et al.*, 2013: table S13). These authors consider differences of less than 1 g without any statistical test; however, shrews can consume two or three times their body mass in food over a 24–h period (Schmidt, 1994). Therefore, we consider our statistical approach more accurate for establishing shifts in body size and for a proper understanding of this field.

Our results showed that *Asoriculus* and *Nesiotites* species show a clear shift towards gigantism, whereas *Crocidura* species do not. Biologically, species that experience shifts in environment or colonize new sites require adaptations for preventing their extinction, and therefore the Island Rule (body mass shifts) has to be understood in this context (Sondaar, 1977; Lomolino, 2005). These adaptations are attained, in the early stages, by phenotypic plasticity of species, and later by genetic assimilation and evolution (Whitman & Agrawal, 2009; Aubret, 2015; Lande, 2015). Body mass is subjected to innumerable selection forces as a result of its close relationship with life-history and fitness-related traits of individuals (e.g. physiology, behaviour, and life-history traits; Calder, 1984). Differences in selective regimes have a high impact on life history and fitness of species, and consequently lead to modifications and adaptations of body mass (Stearns, 1992). Islands show great differences from mainland environments (regarding competition, predation pressure, and resource availability), which trigger distinct growth and survivorship patterns of the species and, consequently, lead to modifications in body mass. Following Life-History Theory, Palkovacs (2003) suggested that small insular mammals evolve towards giant forms principally as a result of low extrinsic mortality. This change triggers a later age at maturity and, in last instance, an increase in body size. In the previously mentioned case, the absence of a body size change in *Crocidura* species from Crete and Sicily appears unusual, but this absence is also observed on other islands (e.g. *Crocidura* sp. from Flores; Van den Hoek Ostende, Van der Berch & Awe Due, 2006).

The body mass evolution on islands is influenced by multiple factors: the biology of the species (e.g. capability and costs of phenotypic plasticity, and genetics), environment (biotic and abiotic characteristics), and contingency (Meiri, Cooper & Purvis, 2008). The biology of a species and its phenotypic plasticity play significant roles in adaptation to new environments. As a result of its genetic basis, constraints at the phylogenetic level may occur (Whitman & Agrawal, 2009); however, phylogenetic restrictions on increasing body mass in *Crocidura* species are highly improbable because large phenotypes are found on islands (see the Sumatran giant shrew, *Crocidura lepidura* Lyon, 1908, with a weight of 18.5 g; Ruedi, 1995) and on the mainland (*C. oliveri odorata* and *C. flavescens*; Table S1). Besides, shrews are *r*–strategists, which makes them ideal founder populations as it favours plasticity/adaptation for dispersal among environments (Whitman & Agrawal, 2009). Moreover, the biology (lifestyle, locomotion, or behaviour) of certain species may influence the magnitude of selective pressure, making some biological groups more susceptible to a particular environmental change. For instance, certain lifestyles may be less exposed to predators, leading to low extrinsic mortality levels. However, at the moment, certain biological aspects (locomotor type and behaviour) are almost unknown for most of the fossil shrew species, and cannot be assessed. On the other hand, traditionally, the characteristics of island ecosystems (area, latitude, isolation, competitors, and predators) are regarded as the main drivers of body mass shifts (Lomolino *et al.*, 2012). In this way, it is observed that: (1) changes in phenotype/adaptations are promoted when the species dwell in different environments, as a result of the difference in their selective regimes (Lande, 2015); and (2) adaptation is favoured when species have restricted gene flow from the original site (Van Buskirk & Arioli, 2005). Particularly on islands, it is noted that gigantism in small mammals is more pronounced on small islands with moderate isolation (restricted flow), where native mammalian predators and competitors are lacking (differing from mainland selective regimes) (Heaney, 1978; Lomolino *et al.*, 2012).

In light of this, we think that the reason for the absence of gigantism in *Crocidura* species from Crete must be sought mainly from differences in the environment (levels of extrinsic mortality and competition, and/or gene flow from the mainland), in comparison with Mallorca and Sardinia. In the case of Sicily, *A. burgioi* may be considered a giant for its large size, and probably the lightweight subspecies of *C. sicula* are normal-sized forms. Nevertheless, we prefer to remain careful in the interpretations of Sicilian species because the weight of the ancestor is not known. For this reason, we restricted our assessment of environmental traits to those species of which the forerunners are known with certainty: *A. similis* from Sardinia, *C. zimmermanni* form Crete, and *Nesiotites* sp. from the Gymnesic Islands. The main ecological traits of the assessed species are

Table 6. Ecological parameters for the habitats of: *Asoriculus similis*, *Crocidura zimmermanni*, and *Nesiotites* species

	Asoriculus similis	*Crocidura zimmermanni*	*Nesiotites species*
Body mass of ancestor (in g)	8.85	8.50	8.85
Gigantism pattern	Yes	No	Yes
Locality	Sardinia	Crete	Gymnesic Islands
Latitude and climate	The same for the three islands (Peel, Finlayson & McMahon, 2007)		
Area of the island	24090 km^2	8336 km^2	3640 km^2
Isolation	≈190–250 km	≈100–150 km	≈200 km
Type of isolation (following Marra, 2005)	Oceanic-like islands of type 1 or type 2 (Pleistocene–Holocene)	Archipelago Oceanic-like islands of type 2 (Early–Middle Pleistocene) and island separated by narrow sea (Late Pleistocene)	Oceanic-like island of type 1 (Miocene–Holocene)
Predators	No mammalian carnivores present with the entrance of *Asoriculus*. *Cynotherium sardoum* Studiati, 1857 arrived later. Birds of prey: *Tyto alba* (Scopoli, 1769)	Otter: *Lutrogale cretensis* (Symeonides & Sondaar, 1975). Birds of prey: *Tyto alba*, *Aegolius funereus* Linnaeus, 1758, and others	No mammalian carnivores on the island. Birds of prey: *Tyto balearica* Mourer-Chauvire, Alcover, Moyà & Pons, 1980; *Aquila* Linnaeus, 1758 species and others
Competitors	*Rhagapodemus* Kretzoi, 1959, *Tyrrhenoglis* Engesser, 1976, several cricetids, and *Talpa* Linnaeus 1758	*Kritimys* Kuss & Misonne, 1968 and *Mus* Linnaeus, 1758	*Hypnomys* Bate, 1918

summarized in Table 6 (body size of the ancestor, current area of the island, isolation distance, latitude and climate, and predators and competitors) (Lomolino *et al.*, 2012). At first sight, the three species do not seem to show marked differences in certain traits (e.g. body mass of ancestor, latitude and climate, and predators and competitors). Terrestrial predators were absent on the Gymnesic Islands, whereas on Crete only the otter *Lutrogale cretensis* (Symeonides & Sondaar, 1975), which principally preyed on fish and crustaceans, was present (Van der Geer & Lyras, 2011). Sardinia is known for the presence of canids and mustelids. However, their appearance after *A. similis* and their low predilection for shrews when other micromammal groups are present (e.g. rodents or lagomorphs) probably prevent specialization in their diet (Table 6; Korpimäki & Norrdahl, 1989). The major consumers of shrews on the mainland are birds of prey, which are well identified in the Mediterranean region (Covas & Blondel, 1998; Donázar *et al.*, 2005), and most likely they also predated on the shrew species on the islands (Adrover, 1972; Masseti, 2009; Weesie, 1987). Land area and the degree of isolation from the mainland are the two traits completely distinct among these islands. Mallorca is the smallest island (42% of the size of Crete and 15% of the size of Sardinia) with similar isolation from the mainland as Sardinia (133–250% further from the mailnland than Crete). These are suggested to be the two most important ecological traits for explaining the gigantism of small extant insular mammals, including shrews (Heaney, 1978; White and Searle, 2007; Lomolino *et al.*, 2012). Gigantism in small mammals is considered to be less conspicuous on large islands because of the larger level of biodiversity and interspecific competition, compared with smaller islands (Heaney, 1978). In our analysis, giant forms are presented on the smallest and on the largest islands (Mallorca and Sardinia), but not on the middle-sized island (Crete). Thus, the size of Crete does not preclude the increment in body size of its shrew species. The competitors of the soricids assessed are rodents and moles (Table 6). The shrew's diet consists primarily of invertebrates (insects) and small vertebrates, complemented with fruits and seeds. Rodents have a more omnivorous diet and moles are specialized in invertebrates found in the soil, such as earthworms and grubs (Henderson, 1994; Schmidt, 1994). However, competitors and predators can also arrive from the mainland, and here is where the degree of isolation plays a role, because the immigration rate depends on the distance of the island from the mainland (MacArthur & Wilson, 1967). Sardinia and the Gymnesic Islands are more isolated than Crete, and, in addition, they show true barriers of water that separate them from the mainland (Table 6). Crete is characterized by the presence of an archipelago between it and the continent (the Aegean Archipelago), and also by time periods during which the islands and mainland were only separated by narrow stretches of sea (Table 6; Marra, 2005). This greater proximity increases the probability of immigration events (MacArthur & Wilson, 1967) and suggests more connections (there might be no restricted flow of individuals from the mainland, and so competitive and predator species might migrate). Although Crete is known for the presence of dwarf mammoths and several species of deer (supposedly adaptive radiation; Caloi & Palombo, 1996; De Vos, 1979; Marra, 2005), the immigration rate also depends on the dispersal capabilities of each species (MacArthur & Wilson, 1967). Certain cases are observed where the barrier is insurmountable for one kind of taxa, but not for others (filter bridges, sweepstake dispersal, and 'pendel' dispersal). Shrews are known for poor oversea dispersal because they have a high metabolism and a tiny body size (Van der Geer *et al.*, 2010). Nevertheless, they were able to cross a filter bridge that connected North Africa and Sicily insuperable for other taxa, disperse to the Canary Islands via a natural raft, and establish themselves in other remote oceanic islands (Dutton & Haft, 1996; Dubey *et al.*, 2008). Moreover, it is observed that current species of shrews frequently colonize islands and archipelagos close to the mainland (Hanski, 1986). Curiously, the subspecies of *C. sicula* from Sicily, the other probable normal-sized species, also had an archipelago between the mainland and its island (Marra, 2005). Another strange fact is that there is no trend towards spectacular gigantism, nor towards adaptive speciation, in the rodent species of Crete. Van den Hoek Ostende *et al.* (2014) considered that climatic factors and the phylogenetic condition of rodent species were responsible for the absence of gigantism, attributing the lack of giant murids to rodent fact that year-round active species maintain an *r*–selected life history under unfavourable environmental conditions there, in contrast with dormice that can enter torpor. In contrast to their view, however, murid body size is not constrained by these life-history traits and phylogeny, because several giant forms are described from extant (*Phloeomys pallidus* Nehring, 1890 or *Crateromys schadenbergi* Meyer, 1895) and extinct (*Canariomys bravoi* Crusafont-Pairó & Petter, 1964 or *Mikrotia magna* Freudenthal, 1976) insular faunas. The absence of body size shifts in almost all micromammals (shrews and rodents) from Crete highlights the importance of environmental traits.

Another distinctive trait of *C. zimmermanni*, aside from its absence of gigantism, is the fact that it lives in the present day. The biological adaptations to insular regimes (body size, life history, locomotion, behaviour, among others) make insular species less competitive than mainland settlers under continental conditions (they moved towards a slow life history with a longer generation time; Köhler, 2010). Therefore, substitutions of faunas (extinctions) occur with the change towards continental conditions and the associated arrival of competitive immigrants from the mainland, especially with extended connections (corridors) (Alcover, Moyà-Solà & Pons-Moyà, 1981; Sax & Gaines, 2008; Sondaar, 1977; Donlan & Wilcox, 2008). *Crocidura zimmermanni* survived faunal exchanges and the arrival of humans and their associated exotic fauna, indicating that it remained competitive even under the changed environmental conditions (selective regimes). Biological studies about its physiology, behaviour, life history, and other biological traits are required for assessing its ability to adapt and shed further light on this issue (Magnanou *et al.*, 2005).

Another interesting result is the gradual increase in size (no fluctuations) over time of *Nesiotites* sp., which is also seen in other small insular species, such as *Hypnomys* sp. (Moncunill-Solé *et al.*, 2014) or *Prolagus*, from Gargano and Sardinia (B. Moncunill-Solé, pers. observ; Moncunill-Solé *et al.* 2016). This is in contrast to the idea that body size changes on islands occur rapidly following colonization, with a subsequent stasis corresponding to a demographic equilibrium and local optimum (Millien, 2006; Cucchi *et al.*, 2014; Aubret, 2015). Several abiotic/environmental factors (e.g. changes in climate) would explain this: for example, the Orkney vole has not presented any stasis, as its environment has been subject to continued anthropological disturbance (Cucchi *et al.*, 2014). Environmental (abiotic) changes do not act exclusively on the evolution of taxa, but biotic factors (such as competition or predation between individuals of different or of the same species) may also come into play (Red Queen hypothesis; Brockhurst *et al.*, 2014; Van Valen, 1973b).

CONCLUSION

The allometric models for reconstructing the body mass of soricid species are significant, excepting the skull measurement (width of occipital condyles, WOC). Femur parameters are considered the best body mass predictors and, contrary to results from studies of other mammalian orders, tooth variables offer similar statistical values of confidence. The use of tibiae as a single body mass proxy is not recommended. The weights of some insular soricid species were estimated (in grams) and allowed us to determine that the widths of molars are not a good proxy, and to instead recommend the use of lower and upper dentitions. The insular *Asoriculus* and *Nesiotites* species (*A. burgioi* from Sicily, 27.54; *A. similis* from Sardinia, 23.68; *Nesiotites* species from the Gymnesic Islands: *N. ponsi*, 14.58; *N. meloussae*, 24.83; *N. hidalgo*, 26–30) showed a larger body mass than *Crocidura* species (*Crocidura* subspecies from Sicily: *C. sicula esuae*, 9.50; *C. sicula sicula*, 8.6; *C. zimmermanni* from Crete, 7–10). For comparison, the body mass of their mainland ancestors was also estimated (*A. gibberodon*, 8.85; *C. kornfeldi*, 8.50). Although insular species of *Asoriculus* and *Nesiotites* show significant differences with their mainland ancestor (*A. gibberodon*), and are considered genuine giants, this is not the case for *Crocidura*. We consider environmental traits to be the main cause of absence or presence of gigantism in shrews, although the biology (phylogeny and lifestyle) may also have a significant role. The greater proximity to the mainland and the presence of an archipelago between Crete and the mainland may have allowed more connections to be made in the past. These connections may have led to the introduction of more competitors and predators from the mainland and the existence of a flow of individuals with the mainland in the past. These particular ecological traits may prevent body size changes towards gigantism in *C. zimmermanni*. Its extant presence, surviving faunal exchanges and the arrival of humans and exotic fauna, may also be indicative of a similar life history to that of mainland species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1 Bivariate regression models in log–log, created between body mass (BM) (in g) and several morphological measures.

Table S1 The species follow an alphabetic order. The following columns are the sample used (*N*), the locomotor type and bibliography [italics indicates that the locomotion is not well-known for this species, but we considered it as terrestrial following Hutterer (1985)], BM (in *g*), and bibliography (all the BM data are from literature, except those obtained from specimens of the NHMUS).

Table S2 Columns: skeletal measurement, and significance of intercept, BM and locomotion respectively (significance level of 0.05).

Figure S1. Bivariate regression models in log-log performed between BM (in g) and: (A) LM/1; (B) WM/1; (C) TRLM/1; (D) AAM/1; (E) TRAAM/1; (F) LM1/; (G) WM1/; (H) TRLM1/; (I) AAM1/; (J) TRAAM1/; (K) FL; (L) FTDp; (M) FAPDd; (N) FTDd; (O) HL; (P) HAPDp; (Q) HTDd; (R) HAPDd; (S) TL; (T) TTDp; (U) TAPDp; and (V) TTDd. Measurements are in mm.

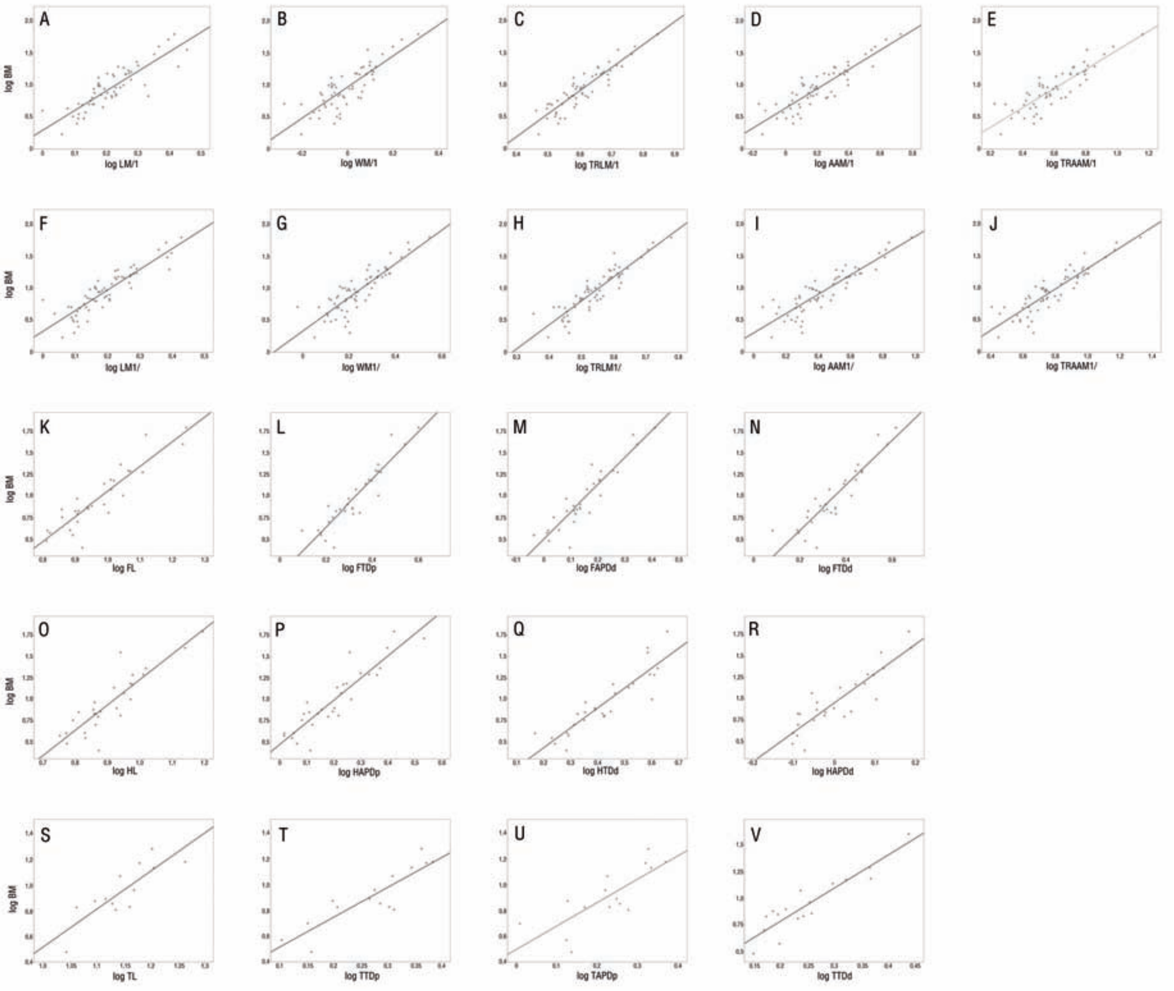

Table S1

SPECIES	N	LOCOMOTION	BIBLIOGRAPHY	BODY MASS (g)	BIBLIOGRAPHY
Anourosorex squamipes	1	Semifossorial	Yu (1993)	35	Silva & Downing (2005)
Anourosorex yamashinai	2	Semifossorial	Yuan *et al.* (2006)	19,345	Yu (1993)
Blarina brevicauda	5	Semifossorial	Ohdachi (1992)	22,8	Silva & Downing (2005)
Chimarrogale platycephalus	1	Semiaquatic	Hutterer (1985)	30	Silva & Downing (2005)
Crocidura attenuata	5	*Terrestrial*		19,1	Silva & Downing (2005)
Crocidura bottegi	8	Terrestrial	Hutterer (1985)	3,2	Silva & Downing (2005)
Crocidura douceti	4	Scansorial	Kingdon *et al.* (2013)	4,3	Silva & Downing (2005)
Crocidura flavescens	11	*Terrestrial*		51	Silva & Downing (2005)
Crocidura foxi	1	*Terrestrial*		21	Silva & Downing (2005)
Crocidura fulvastra	10	*Terrestrial*		15	Silva & Downing (2005)
Crocidura fuscomurina	7	*Terrestrial*		3	Silva & Downing (2005)
Crocidura glassi	2	*Terrestrial*		18,5	Demeter & Topál (1982)
Crocidura gracilipes	2	*Terrestrial*		8,65	Silva & Downing (2005)
Crocidura gueldenstaedtii	3	*Terrestrial*		8,67	Silva & Downing (2005)
Crocidura hildegardeae	2	*Terrestrial*		9,5	Silva & Downing (2005)
Crocidura hirta	3	*Terrestrial*		16	Silva & Downing (2005)
Crocidura lasiura	26	*Terrestrial*		14,8	Silva & Downing (2005)
Crocidura leucodon	33	*Terrestrial*		7,8	Silva & Downing (2005)
Crocidura Lucina	1	*Terrestrial*		20	Demeter & Topál (1982)
Crocidura luna	3	*Terrestrial*		14,5	Smith *et al.* (2003)
Crocidura lusitania	1	*Terrestrial*		2	Silva & Downing (2005)
Crocidura montis	12	*Terrestrial*		14,49	Silva & Downing (2005)
Crocidura nana	2	*Terrestrial*		3,5	Demeter & Topál (1982)
Crocidura negligens	1	*Terrestrial*		12	Okie & Brown (2009)
Crocidura olivieri odorata	3	Terrestrial	Jenkins *et al.* (1998)	61,5	Silva & Downing (2005)
Crocidura pasha	1	*Terrestrial*		6,5	Smith *et al.* (2003)
Crocidura planiceps	4	*Terrestrial*		2,5	Silva & Downing (2005)
Crocidura poensis	3	*Terrestrial*		16,7	Silva & Downing (2005)
Crocidura rapax tadae	3	*Terrestrial*		6,3	Fang & Lee (2002)
Crocidura russula	19	Terrestrial	Jenkins *et al.* (1998)	6,4	Silva & Downing (2005)
Crocidura shantungensis	7	*Terrestrial*		5	Hungarian Natural History Museum
Crocidura somalica	3	*Terrestrial*		11,5	Silva & Downing (2005)
Crocidura suaveolens	20	*Terrestrial*		6,69	Silva & Downing (2005)
Crocidura viaria	1	*Terrestrial*		17	Silva & Downing (2005)
Cryptotis parva	3	Semifossorial	Swiderski (1991)	4,89	Silva & Downing (2005)
Diplomesodon pulchellum	1	Psammophilic	Hutterer (1985)	11,17	Volodin *et al.* (2012)
Episoriculus caudatus	7	Terrestrial	Molur (2008)	9,124	Smith *et al.* (2003)
Episoriculus fumidus	6	Terrestrial	Smith & Johnston (2008)	6,73	Smith *et al.* (2003)
Neomys anomalus	14	Semiaquatic	Hutterer (1985)	13,6	Silva & Downing (2005)
Neomys fodiens	15	Semiaquatic	Hutterer (1985)	15,14	Silva & Downing (2005)
Notiosorex crawfordi	1	Terrestrial	Hutterer (1985)	3	Silva & Downing (2005)
Sorex alpinus	13	Scansorial	Hutterer (1985)	6,215	Silva & Downing (2005)
Sorex araneus	23	Semifossorial	Ohdachi (1992)	7,14	Silva & Downing (2005)

Sorex caecutiens	5	Terrestrial	Ohdachi (1992)	7	Silva & Downing (2005)
Sorex camtschatica	1	*Terrestrial*		5	Yudin (1989)
Sorex cinereus	3	Terrestrial	Ohdachi (1992)	3,72	Silva & Downing (2005)
Sorex coronatus	6	*Terrestrial*		9,65	Silva & Downing (2005)
Sorex daphaenodon	1	*Terrestrial*		6,79	Silva & Downing (2005)
Sorex gracillimus	1	Terrestrial	Ohdachi (1992)	5,06	Smith *et al.* (2003)
Sorex isodon	1	Semifossorial	Kooij & Solheim (2002)	10,5	Smith *et al.* (2003)
Sorex minutissimus	1	*Terrestrial*		1,7	Silva & Downing (2005)
Sorex minutus	10	Terrestrial	Hutterer (1985)	3	Silva & Downing (2005)
Sorex monticolus	4	Terrestrial	Swihart (2003)	5	Silva & Downing (2005)
Sorex palustris	4	Semiaquatic	Hutterer (1985)	12,95	Silva & Downing (2005)
Sorex raddei	1	*Terrestrial*		10	Smith *et al.* (2003)
Sorex roboratus	1	*Terrestrial*		9,124	Smith *et al.* (2003)
Sorex trowbridgii	2	Semifossorial	Swihart (2003)	4,49	Silva & Downing (2005)
Sorex tundrensis	6	*Terrestrial*		7,5	Smith *et al.* (2003)
Sorex unguiculatus	1	Semifossorial	Hutterer (1985)	9,9	Silva & Downing (2005)
Sorex vagrans	3	Terrestrial	Samuels (2007)	5,66	Silva & Downing (2005)
Sorex veraepacis	1	Terrestrial	Swiderski (1991)	7,5	Silva & Downing (2005)
Soriculus nigrescens	9	Fossorial	Hutterer (1985)	9,9	Smith *et al.* (2003)
Suncus etruscus	2	*Terrestrial*		3,97	Silva & Downing (2005)
Suncus murinus	8	Terrestrial	Meier *et al.* (2013)	39,5	Silva & Downing (2005)

The species follow an alphabetic order. The following columns are the sample used (N), the locomotor type and bibliography (italics indicates that the locomotion is not well-known for this species, but we considered it as terrestrial following Hutterer (1985)), BM (in g), and bibliography (all the BM data are from literature, except those obtained from specimens of the NHMUS).

Table S2

	Significance	
	BM	Locomotion
FL	0,000	0,745
FTDp	0,000	0,286
FAPDd	0,000	0,832
FTDd	0,000	0,369
HL	0,000	0,779
HAPDp	0,000	0,840
HTDd	0,000	0,085
HAPDd	0,000	0,074
TL	0,000	0,272
TTDp	0,000	0,824
TAPDp	0,006	0,521
TTDd	0,000	0,287

Columns: skeletal measurement, and significance of intercept, BM and locomotion respectively (significance level of 0.05).

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Chapter 10

Discussion

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DISCUSSION

The central position and the importance of BM in organismal biology originated the keen interest of paleontological researchers for estimating this trait in extinct species. BM (BS proxy) plays a main role in paleontological studies related to functional morphology, metabolic physiology and energetics, evolution of body proportions, paleoecology, taphonomic processes, tempo and mode of size evolution, etc. (for more details see Damuth and MacFadden 1990b). The paleontological perspective of BS shift of insular small mammals is the central aim of the present PhD Thesis. The ensuing discussion is ordered following the specific goals proposed in chapter 2. In a first section (10.1), we evaluate the BM regression models obtained (proxies, statistical variables, among others). In a second section (10.2), we show the BMs estimated for some insular species and their mainland ancestors, and we compare them to previous estimations performed by other authors and to data of extant fauna. Finally, the last section (10.3) assesses the IR from different perspectives: 1) it is established the presence of giants (or not) in some Mediterranean Islands; 2) it is analyzed which ecological parameters of the island trigger the observed BS shift (comparing one island with another); 3) it is evaluated the evolutionary pattern of BS shift using material of the same species (or anagenetic species) from different geological periods; and 4) it is assessed if the changes in BS in insular small mammal species are associated with a change in LH.

10.1. Body mass regression models for small mammals

To date, most of the BM predictive models (equations) have been developed for large mammals (primates, carnivores, elephants or artiodactyls, among others) (Gingerich et al. 1982, Legendre and Roth 1988, Damuth and MacFadden 1990, Schwartz et al. 1995, Christiansen 2004, Mendoza et al. 2006, Köhler 2010, Tsubamoto et al. 2016, among others). Meanwhile, for small mammals, extensive BM models have only been carried out for rodents (Legendre 1986, Parra and Jaegers 1998, Bicknevicius 1999, Hopkins 2008, Rinderknecht and Blanco 2008, Millien and Bovy 2010, among others). Nonetheless, lagomorphs or insectivores have elementary BM predictive models that have been set up as a secondary part of some investigations, but without much statistical accuracy and with only few measurements (see Bloch et al. 1998, Quintana Cardona 2005, Quintana et al. 2011). This results in a wide scientific gap for thoroughly investigating the biology of fossil small mammals. Our studies are focused on developing BM predictive models extensively through statistics for small-sized mammals. We provide the first equations for estimating the BM of lagomorphs and soricids and new allometric models for the order Rodentia (see chapters 4, 6 and 9).

Bivariate and multiple regression models

Certain skeletal measurements from different sources (teeth, skull and long bones) were selected as BM proxies for conducting our research. Historically, teeth (principally molars) are the most frequently used items for estimating BM of extinct species for two reasons. Firstly, teeth are the most commonly preserved elements in the fossil record (Naples 1995, Gingerich 1977a). Enamel is the tissue with the best preservation potential (even over millions of years), a consequence of its particular mineral composition (Hillson 2005). Secondly, teeth are the main diagnostic elements of mammals and, consequently, are vital in paleontological studies (Benton 2005). Most of the extinct species of mammals are only represented by dental or cranio-dental remains, because the recovered postcranial bones cannot be assigned at species level (e.g. the species of *Hoplitomeryx* Leinders 1983, see Mazza and Rustioni 2011). This becomes evident in the great amount of studies carried out with teeth as the main BM proxy (Gingerich 1977b, Creighton 1980, Gingerich et al. 1982, Gingerich and Smith 1984, Legendre 1986, 1989, Conroy 1987, Legendre and Roth 1988, Damuth 1990, Fortelius 1990, Janis 1990, Jungers 1990, MacFadden and Hulbert 1990, Martin 1990, Van Valkenburgh 1990, Parra and Jaeger 1998, Schwartz et al. 1995, Mendoza et al. 2006, Hopkins 2008, Millien and Bovy 2010, Freudenthal and Martín-Suárez 2013). Also the skull is frequently used for estimating the BM of extinct species. This is a consequence of its role as teeth support and of the aforementioned reasons (Janis 1990, Van Valkenburgh 1990, Millien 2008, Rinderknecht and Blanco 2008, Bover et al. 2010b, Millien and Bovy 2010). Some time later, scientific studies began focusing on the use of other skeletal bones to develop predictive regression models, such as long bones, metapodials or tarsi (Gingerich 1990, Roth 1990, Ruff 1990, Scott 1990, Van Valkenburgh 1990, Anyonge 1993, Köhler 1993, Alberdi et al. 1995, Martínez and Sudre 1995, Bicknevicius 1999, Christiansen 1999, 2004, Egi 2001, Köhler and Moyà-Solà 2004, Palombo and Giovinazzo 2005, Mendoza et al. 2006, Köhler 2010, Millien and Bovy 2010, De Esteban-Trivigno and Köhler 2011, Tsubamoto et al. 2016). Our results from small-sized mammals show that regardless of the nature of source (teeth, skulls or long bones), the models obtained in our analyses are statistically significant ($p < 0.05$) (excepting the WOC variable in soricids, see chapter 9). In order to select the best BM proxy, Reynolds (2002) pointed out that the best estimator does not only depend on the accuracy of the model (significance and statistical values), but also on a subjective judgment of the BM estimations obtained for each particular species (or genus). For this reason, particular emphasis should be placed on statistical parameters (r^2, %PE, SEE, among others) of the allometric models, which inform us about the reliability and accuracy; but also on the results (BM values) of testing these equations specifically to the species that we studied. In this way, we should be able to determine that some regression models are better than others.

In assessing the nature of the proxies, the results from rodent species (chapter 4: Tab. 1) show that the predictive BM models performed with measurements of tooth, skull and long bone, have minimal differences in their statistical accuracy (r^2 values around 0.9 and low %PE values) (previously observed by Millien 2008: Tab. 1 and Millien and Bovy 2010: Tab. 1). When these equations are tested using certain fossil species (chapter 4: Tab. 2), specifically dental parameters predicted the most extreme values of BM (the lowest or the highest, depending on the species) (chapter 4: Fig. 3). However, a clear pattern of outliers is not observed. Millien and Bovy (2010: Tab. 1 and 3) noticed a variation around 400-500 kg depending on the nature of the proxy (teeth or long bones) when they estimated the BM of the giant extinct rodent *Phoberomys pattersoni* Bondesio and Bocquentin Villanueva 1988 (see also Rinderknecht and Blanco 2008, Millien 2008). In the case of soricids, regression models show comparable statistical parameters of reliability and accuracy irrespective of the measurement (chapter 9: Tab. 4). Here, however, we cannot test the long bone models in the fossil record because these elements are rarely studied and are not identified at species level (Reumer 1981, 1984, 1986, Rofes and Cuenca-Bescós 2006, 2011, Furió and Angelone 2010, Rofes et al. 2012, among others). As regards the lagomorphs (chapter 6: Tab. 3 and 4), it is observed that the models performed with dental measurements provide lower values of r^2 and higher %PE than those obtained from postcranial elements (femora, humeri and tibiae). When lagomorph models are tested with fossil species, clear discrepancies can be noticed (chapter 6: Fig. 2 and chapter 7: Fig. 2). In large mammals, the BM estimations based upon limb measurements appear to be substantially more reliable than those performed with cranial or dental measurements (%PE below 30 are rare)

(Legendre and Roth 1988, Damuth and MacFadden 1990b, Janis 1990, Scott 1990). Vertebrates do not transmit BM through their skulls or teeth, and accordingly there is not any biomechanical reason for expecting a direct or predictable relationship (Hylander 1985). Teeth have been subjected to much more adaptive evolution than postcranial bones and their dimensions may denote differences related to diet or other biological traits (Damuth 1990). In contrast, weight-bearing elements of the appendicular skeleton should be more reliable BM estimators, especially postcranial joint size (Jungers 1988). Several authors evinced the discrepancy between teeth and postcranial bones as BM proxies (Jungers 1990, Millien and Bovy 2010, among others), especially in insular species (e.g. *Palaeoloxodon falconeri*, *Oreopithecus bambolii* and some dwarf hippopotami; see Maglio 1973, Moyà-Solà and Köhler 1997, Gould 1975 respectively). This discordant pattern between cranio-dental and postcranial measurements is obvious in our results from small mammals. Therefore, and because of the absence of a direct functional principle that relates cranio-dental variables to a BS increase (Fortelius 1990), we suggest that postcranial bones are better BM proxies than dental parameters in small mammals.

Within the long bones, various parameters are used as estimators (length and diameters). BM loads and reaction forces are proportional to the area of the transversal sections but not to its length (Currey 2006). In line with this principle, several studies in large mammals pointed out that diameters or perimeters (robustness) of long limb bones are better BM proxies than length (Scott 1990, Mendoza et al. 2006, Millien and Bovy 2010). Our results from rodents and soricids are in accordance with these observations (length measurements have lower r^2 and greater %PE, see chapters 4 and 9 respectively). In contrast, in the case of lagomorphs, r^2 of length of long bones is similar to other limb measurements and the %PE is slightly higher (chapter 6: Tab. 4). The use of length of humeri, femora and tibiae has provided satisfactory results in fossil lagomorphs (chapter 8). However, it must be taken into account that, generally, length is a difficult measurement to take because of the great fragmentation of long bones caused by taphonomic processes and screen-washing procedures. Additionally, it is also observed that zeugopods (ulna, radius, tibia and fibula) are the limb bones that are more modified for locomotion and habitat preference of species (Damuth and MacFadden 1990b, Scott 1990, Köhler 1993). Their reliability as proxies is worse because they do not only represent BM but also their locomotor adaptations (Scott 1990). The results of tibia models in the three groups assessed are different. In the case of rodents, it can be observed that tibia models have high coefficients of determination (r^2), but also higher values of %PE (chapter 4: Tab. 4). With regards to lagomorphs, tibia models show statistical values similar to femur and humerus models. However, extreme predictions are obtained when applied to some fossil species (*N. rex* in chapter 6, but also see the results of *P. sardus* in chapter 7). In the case of soricids, tibia models have low values of r^2 but %PE similar to those of femora and humeri. Our results are not entirely in line with trends of large mammals, particularly in the case of lagomorphs. This may be due to the fact that most of the lagomorph species are specialized in a specific type of locomotion (racing and jumping) (Chapman and Flux 1990), while in the case of rodents and soricids the range of locomotor behaviors is wider (Hutterer 1985, Samuels and van Valkenburgh 2008). Nonetheless, the regression models of stylopods (femora and humeri) are more accurate: lower predictive error (%PE) and higher goodness-of-fit statistics (r^2). Thus, we suggest that these bones (stylopods) are preferable as BM proxies.

The use of teeth (generally speaking, cranio-dental variables) for predicting BM is less recommendable, but as a result of their good preservation and easy identification, they are frequently the only available and/or useful elements (see previous references). This happens in the case of the family Soricidae (chapter 9). Here, BM estimation models are performed using upper and lower teeth and no significant differences are detected (neither in statistical parameters nor tests on fossils, see chapter 9: Tab. 4 and 5). Moreover, these results provide evidence that width of teeth is less reliable than other parameters because this measurement is highly influenced by the orientation of the tooth (Van den Hoek Ostende, pers. comm.). This observation in soricids (low reliability of tooth width) is in agreement with the patterns observed in large mammal groups (Damuth 1990, Fortelius 1990, Janis 1990, Schwartz et al. 1995). On the other hand, the only cranial measurement used as BM proxy in our investigations is the width of occipital condyles (WOC). It gives impressive statistical results in rodents and lagomorphs (the same as in artiodactyls, see Köhler and Moyà-Solà 2004), while in soricids the model is considered invalid as a result of the low number of individuals (N). Nevertheless, their use as BM proxy in the paleontological field is hampered by the degree of skull preservation. Because of its fragility, the skull is one of the first elements of the skeleton to break.

As a result of the large N of our analyses, we decided in several occasions to carry out regression models using more homogeneous groups (taking into account the locomotor habits or the phylogeny of the species). In the case of rodents and lagomorphs, we decided to split the large data-base when assessing the teeth variables, because the several families or suborders have specific dental formulae (Hillson 2005). This is not the case for soricids (Family Soricidae), where all species included in the analysis have the same dental formula (Hillson 2005). It is observed in rodents that some particular families (such as Sciuromorpha) show better statistical results than the heterogeneous model (model that includes all species), but this does not occur in other families (e.g. Muridae). These differences may be a consequence of the higher degree of heterogeneity of these latter groups and that dentition is highly specialized at a clade level (Hopkins 2008). In the case of lagomorphs, the trends among BM and dental parameters of the ochotonids and leporids (families of lagomorphs) are significantly different ($p < 0.05$) (chapter 6: Fig. S1). Furthermore, locomotion may also have an effect on the shape and size of postcranial elements (Scott 1990, Köhler 1993, Samuels and van Valkenburgh 2008). It was only possible to observe significant differences among some groups ($p < 0.05$) with different locomotion in the case of lagomorphs (modification of distal humerus of the fossorial or semifossorial species), but not in others (rodents and soricids). In this respect, the great prevalence of terrestrial species in the database used and the lack of knowledge of the biology (life style) of many species may play a key role. At statistical level, we also developed multiple models which are more satisfactory than bivariate ones in all the groups assessed (see respective chapters). Multiple models are less constrained by ecological adaptations of species and its phylogenetic legacy; they compensate for this using several measurements of the skeleton without redundant information (stepwise process) (Quinn and Keough 2002, Mendoza et al. 2006; for more details see chapter 3). However, due to the nature of fossils, multiple equations are of only little utility. Micromammals are mainly obtained by screen-washing procedures (López-Martínez 1989). On the one hand, these techniques lead to the disconnection of elements of the same individual. On the other hand, depending on the site and fossilization, they contribute to the fragmentation of bones. For this reason, only in some particular cases could these multiple models be applied to the fossil individuals/species (e. g. Bover et al. 2010b, Michaux et al. 2012).

To sum up, our results from small mammals indicate that several skeletal elements and variables are preferable as BM proxies (diameters of stylopods) while others are less recommendable (such as teeth, zeugopods or length of long bones). Sometimes, however, these latter elements are the only available parts of a species (especially teeth). The BM can be estimated from their dimensions, but these results must be interpreted with caution. However, we must also take into consideration that the reliability as BM proxy also depends on the species concerned. Although zeugopods are generally less preferred, they can be good BM proxies in some group in particular (this can be seen in the results of tibia as a proxy in *N. rex* and *P. sardus*). Therefore, it is recommendable to estimate BM of fossil species using the largest number of skeletal variables (including teeth and bones) when possible. Most often, the phylogeny or locomotion of extinct species is not well-known. Consequently, some skeletal variable might not only represent the BM of the individual but also other biological attributes leading to over- or underestimations of their BM. Estimating the BM with multiple parameters permits to detect strange patterns of some variables and to discard them (see below).

10.2. Body mass estimation of fossil species of small mammals

The previously developed models are used for predicting the BM of several fossil species. We assess the weight of certain insular species and, as far as possible, of their ancestors or relatives. For rodents and lagomorphs, our predictions are based on measurements of dental and postcranial elements, while for soricids, we only use dental parameters. For some of these species, this is the first time that BM is estimated. The results of the estimations (in g) carried out in this research are presented in Table 10.1 (column: Moncunill-Solé et al. estimation). For more details, see previous chapters.

In some cases, it is observed that certain measurements predicted BMs that are not in line with the other estimations (other measurements) (similiar results are seen in Millien 2008: Tab. 1, Millien and Bovy 2010: Tab. 3). For the following reasons, we decide to exclude them for the calculation of the species average. In the case of *C. bravoi*, it is observed that the predictions made with WOC are far below the other estimations (around 500-900 g lower) (chapter 4: Tab. 2). Surely, this species does not follow the same allometric relationship (between BM and this trait) observed in extant species of rodents. The reason of this peculiarity of *C. bravoi* is not known currently, but we cannot rule out that insular ecological regimes may have played a role here (e.g. see the trend in *Myotragus balearicus*, Köhler and Moyà-Solà 2004). With regard to rodents and lagomorphs, it is noticed that, in general, some measurements of humerus are conflictive. Both species of *Canariomys* Crusafont-Pairó and Petter 1964 and *Hypnomys* show a high humeral epicondylar index (ratio of width of distal humerus and its functional length), suggesting a fossorial or semifossorial lifestyle (Samuels and van Valkenburgh 2008). Distal humeral epiphysis of *N. rex* and *P.* cf. *calpensis*, and proximal humeral epiphysis of *P. figaro* and *P. sardus* provided over or underestimations of BM. These groups of mammals (rodents and lagomorphs) are suggested to have digging skills, though generally the locomotor habits of the assessed extinct species have not been defined accurately (e.g. *Prolagus* sp. Pomel 1853 are only represented by one extant relative in the allometric model, *Ochotona* sp. Link 1795). In general, several insular species of small mammals adapt to their new environments by searching for fallback (alternative) resources of the soil (Michaux et al. 2012, Quintana Cardona and Moncunill-Solé 2014). It is likely that the humeral dimensions of these individuals do not only represent their BM, but also their locomotion and life style. Thus, we consider that humeral parameters may reflect more the life style than BM in these species. In lagomorphs, it is also observed that teeth predict either the lowest or the highest BM values (*N. rex*, *P. apricenicus*, *P.* cf. *calpensis*, *P. figaro* and *P. sardus*). Of special interest is the contradictory trend observed between the BM estimations done by postcranial bones and by teeth in the case of *P. sardus* (chapter 7: Fig. 2). The genus *Prolagus* (mainland and insular species) is characterized by the coalescence (fusion) of the M3 with the M2 (Dawson 1969), and consequently these species do not follow the same general allometry of teeth of typical extant lagomorphs. Moreover, Angelone (2005) suggested that it is probable that the modifications of dental morphology

Table 10. 1. BM estimations (in g) of the species assessed in this PhD Thesis; and previous BM estimations (in g) done by other authors.

Species	Moncunill-Solé et al. estimation	Previous estimations		
	BM (in g)	BM (in g)	Measurement	Reference
ORDER RODENTIA				
Canariomys bravoi	1571.3	1900 - 2300	First molar	Michaux et al. (1996)
		758 - 871	Lower tooth row length	Michaux et al. (2012)
Canariomys tamarani	1010.7	1350	First molar	Michaux et al. (1996)
		633 - 824	Lower tooth row length	Michaux et al. (2012)
		750 - 1200	Head-body length	López-Martínez and López-Jurado (1987)
Hypnomys morpheus	232.7	173 - 284	Cranio-dental measurements	Bover et al. (2010b)
		194.3 - 227	Lower tooth row	Van der Geer et al. (2013)
Hypnomys onicensis	201.5	-	-	-
Mikrotia magna	1300 – 1900 (depending on fissure)	400.2	Anteroposterior diameter of the lower incisor	Millien and Jaeger (2001)
Muscardinus cyclopeus	101.7	-	-	-
ORDER LAGOMORPHA				
Prolagus apricenicus	282.2 - 600 (depending on fissure)	-	-	-
Prolagus cf. *calpensis*	319.7 - 363.6	-	-	-
Prolagus figaro	400 - 435 (depending on the site)	356	Dental parameters	Van der Geer et al. (2013)
Prolagus sardus	500 - 525 (depending on site)	800	?	Sondaar and Van der Geer (2000)
		300 - 580 g	Teeth and postcranial elements	Van der Geer et al. (2013)
Nuralagus rex	8241.5	12000	Teeth and postcranial elements	Quintana et al. (2011)

FAMILY SORICIDAE				
Asoriculus burgioi	27.5	-	-	-
Asoriculus gibberodon	8.9	9.28	m1 area	Lomolino et al. (2013) Van der Geer et al. (2013)
Asoriculus similis	20.4	-	-	-
Crocidura kornfeldi	8.5	11.4	m1 area	Van der Geer et al. (2013)
Crocidura sicula esuae	9.5	11.96	m1 area	Lomolino et al. (2013)
Crocidura sicula sícula	8.6	-	-	-
Crocidura zimmermanni	7 - 10 (depending on site)	11 - 15 (depending on site)	m1 area	Van der Geer et al. (2013)
Nesiotites ponsi	14.6	21.5	m1 area	Van der Geer et al. (2013)
Nesiotites aff. *Ponsi*	20.3	36.2	m1 area	Van der Geer et al. (2013)
Nesiotites meloussae	24.8	-	-	-
Nesiotites hidalgo	26 - 30 (depending on site)	41.97	m1 area	Lomolino et al. (2013)
		36.2 - 43.52 (depending on site)	m1 area	Van der Geer et al. (2013)

Columns: Species, Moncunill-Solé et al. estimation [BM (in g) estimated in the research studies of this PhD Thesis]; Previous estimations [BM (in g), the measurement that they used and the reference of the research]. The solid lines separate different species, the dotted lines separate different BM estimations of the same species done by different authors.

observed in insular endemic species of *Prolagus* was associated with a change of the movements of mastication and, hence, in the mandibular mechanics. Thus, teeth are not recommendable items for predicting the weight of extinct *Prolagus* and insular species of lagomorphs. The exhaustive study of *Prolagus* from Sardinia has allowed us to conclude that certain measurements are better predictors (FL, TAPDp, TTDp, TTDd and HTDd) than others, which overestimate the BM of the species (HAPDp and FTDp). This should be taken into account in future BM predictions for *Prolagus*. Finally, in the case of soricids, it is observed that, as discussed above, the width of first molars provides erratic BM predictions (lower and higher values). This measurement is highly influenced by the orientation of the teeth. Its low reliability as BM proxy has previously been observed in large mammals and it is ruled out in average calculations (Damuth 1990, Fortelius 1990, Janis 1990, Schwartz et al. 1995).

Body masses of fossil small mammal species: comparison with previous body mass estimations

Our BM results were compared to previous estimations made by several authors. In order to facilitate the interpretation of comparisons, all the information (Moncunill-Solé et al. estimations and previous estimations done by other authors) is summarized in Table 10.1.

Michaux et al. (1996, 2012), based on dental measurements, predicted lower or higher values for *C. bravoi* and *C. tamarani* than our estimation. Notice, in this case, the high variability of BM estimations using different dental measurements (Tab. 10.1), which is in line with the results of Millien (2008) and Millen and Bovy (2010). However, the estimation of López-Martínez and López-Jurado (1987) for *C. tamarani*, based on head body length, lies within the range of our results. In the case of *H. morpheus*, previous predictions published by Bover et al. (2010b) and Van der Geer et al. (2013) coincide with our values (Tab. 10.1), though they used cranio-dental and tooth row measurements. Millien and Jaeger (2001) worked with lower incisor measurements as proxies and obtained BM predictions markedly lower than ours for *M. magna* (Tab. 10.1). For *H. onicensis* and *M. cyclopeus*, previous weight estimations have not been undertaken.

When comparing the results of lagomorphs, Van der Geer et al. (2013) provided values of BM more or less in line with our own predictions for *P. figaro* and *P. sardus*. However, a previous study by Sondaar and Van der Geer (2000) suggested a BM for *P. sardus* that almost doubles our BM prediction (Tab. 10.1). They did not clarify in the text the element used for performing the analysis. Finally, the authors that erected the species *N. rex* (Quintana et al. 2011) suggested that this species was 4000 grams heavier than our results, using teeth and postcranial proxies (Tab. 10.1). No one had estimated previously the BM of *P. apricenicus* and *P.* cf. *calpensis*.

From these comparisons (rodents and lagomorphs), it is worth pointing out that weight estimations performed with teeth and postcranial elements provide very different results. As stated previously, teeth are less recommendable BM estimators because of the absence of a direct and close relationship with BM. Moreover, in our case, it is important to highlight that insular species show significant modifications of the teeth and the dentognathic feeding apparatus. Specifically a reduction or loss of dental pieces and an increase of hypsodonty is observed (for more details see Van de Geer 2014). Thus, some species of insular rodents and lagomorphs show molars with more complex crowns and enamel folds as well as a modification of the relative proportions of some dental features (Freudenthal 1976, Angelone 2005). Some species, such as *M. magna*, used its incisors for digging holes in the soil (Parra et al. 1999). The low reliability of dental regression models, the erratic BM predictions obtained in insular species (see estimations in *C. bravoi* by other authors) and the extensive modifications of these items as a result of their ecological regimes, rule out teeth as reliable BM proxies for insular rodents and lagomorphs. Instead, our predictions based on several postcranial elements (excluding those related with specific lifestyle modifications) provide more accurate BM values for these species. However, it is important to notice that the most important differences between dental and postcranial estimations are found in the largest species (*C. bravoi*, *C. tamarani* or *P. sardus*; or see also Millien and Bovy 2010), while in the case of the smallest (e.g. *H. morpheus* or *P. figaro*) the differences are not so marked. This may be consequence of two not mutually exclusive facts. On the one hand, the largest insular species are the more modified than smaller ones, and consequently the allometric relationship between teeth and BM is less precise than in smaller species. On the other hand, this may be a problem of scale: large individuals can accommodate either large or small teeth, but small individuals do not have room for large teeth (constrained for their BS). Independently of the reason or the reasons, our results indicate that BM estimations obtained with dental measurements are more reliable in small than in large insular individuals.

Contrary to rodents and lagomorphs, striking changes in teeth (lost of molars or antemolars, or increase of their complexity) in insular species of shrews have not been described with the exception of *N. hidalgo*, which lost the fourth antemolar (Reumer 1981, 1986, Hutterer 1991, Van der Geer et al. 2010, Van der Geer 2014). Based on this observation and because of the lack of knowledge at the specific level of postcranial material of soricids, we decide to estimate the BM of species of this group using dental parameters. In the case of soricids, the BMs of certain species have only been predicted by Lomolino et al. (2013) and Van der Geer et al. (2013). Their results are more or less in line with ours for some of the species (*A. gibberodon*, *C. kornfeldi* and *C. sicula esuae*; with differences of 2-3 g), but differences are more important in others (*C. zimermmanni* and *Nesiotites* sp.; with differences of 5-12 g) (Tab. 10.1). The weights of *A. burgioi*, *A. similis*, *C. sicula sicula* and *N. meloussae* have not been estimated previously. The estimations of the other authors are performed with general equations of teeth that include data of species from different families (Soricidae, Talpidae, Erinaceidae, Macroscelididae and Tupaiidae) (Bloch et al. 1998). Dental formulae differ among these families (Hillson 2005), implying distinct relationships between BM and tooth dimensions (Janis 1990). Our models are exclusively based on soricid species and, thus, they better define the relationship between dental parameters and BM for this group. Hence, we consider our BM predictions more accurate.

Body masses of fossil small mammal species: comparison with extant relative species

Of special concern is the comparison of BMs among the extant and fossil species. In order to facilitate the interpretation, we have elaborated several tables with all the information (BM of fossil and extant species): see Table 10.2 for rodents, Table 10.3 for lagomorphs and Table 10.4 for soricids.

The current BM range of rodents is very broad from the Baluchistan pygmy jerboa (3.75 g) to capybara (40-60 kg), although the average weight of rodents lies somewhere between 10 and 100 g (Silva and Downing 1995). The existence of large rodents is well-known, including species of beavers, pacas, porcupines, coypus, springhares, marmots and squirrels (Tab. 10.2). Several South American fossil rodents were heavier than extant species (Sánchez-Villagra et al. 2003, Rinderknecht and Blanco 2008, Millien 2008). The fossil rodent species assessed here belong to two families: Muridae (*Canariomys* and *Mikrotia*) and Gliridae (*Hypnomys* and *Muscardinus* Kaup 1829). At present several extant species of murids have BMs comparable to *Canariomys* and *Mikrotia*, principally from islands [*Hypogeomys antimena* Grandidier 1869, *Mallomys rothschildi* Thomas 1898, *Papagomys armandvillei*

TABLE 10.2. Comparative table of the BM of the fossil rodent species assessed in our research and the BM of the largest extant species (excepting averages, Baluchistan pygmy jerboa, house dormouse and rats).

Fossil species				Extant species			
Scientific name	BM			BM	Scientific name	Common name	Origin
		Small BS					
			■	3.75 g	*Salpingotulus michaelis*	Baluchistan pygmy jerboa	Mainland
			■	10-100 g	The average weight of rodents		Mainland
			★	10-20g	*Mus musculus*	House mouse	Mainland
Muscardinus cyclopeus	101.7 g	●	●	75-100 g	*Eliomys quercinus*	Garden dormouse	Mainland
Hypnomys onicensis	201.5 g	●	★	100-200g	*Rattus rattus*	Black rat	Mainland
Hypnomys morpheus	232.7 g	●	●	150-200g	*Glis glis*	Fat dormouse	Mainland
			★	200-400g	*Rattus norvegicus*	Brown rat	Mainland
Canariomys tamarani	1 kg	★					
Mikrotia magna	1.3-1.9 kg	★	★	1-1.23 kg	*Mallomys rothschildi*	Rothschild's woolly rat	New Guinea Island
Canariomys bravoi	1.5 kg	★	★	1-1.5 kg	*Cricetomys gambianus*	Gambian pouched rat	Mainland
			★	1.2 kg	*Hypogeomys antimena*	Malagasy giant rat	Madagascar Island
			★	1.2 kg	*Papagomys armandvillei*	Flores giant rat	Flores Island
			★	2.6 kg	*Phloeomys pallidus*	Northern Luzon giant cloud rat	Luzon Island
			■	3 kg	*Pedetes capensis*	South African springhare	Mainland
			■	4.1 kg	*Marmota caudata*	Long-tailed marmot	Mainland
			■	4.3 kg	*Petaurista alborufus*	Red and wite giant flying squirrel	Mainland
			■	5-9 kg	*Myocastor coypus*	Coypu	Mainland
			■	7.23 kg	*Marmota caligata*	Hoary marmot	Mainland
			■	8 kg	*Cuniculus paca*	Lowland paca	Mainland
			■	8 kg	*Marmota sibirica*	Tarbagan marmot	Mainland
			■	12-18 kg	*Hystrix indica*	Indian crested porcupine	Mainland
			■	12-20 kg	*Hystrix africaeaustralis*	Cape porcupine	Mainland
			■	23 kg	*Hystrix javanica*	Sunda porcupine	Mainland
			■	13-25 kg	*Castor fiber*	Eurasian beaver	Mainland
			■	15-35 kg	*Castor canadensis*	North American beaver	Mainland
			■	40-60 kg	*Hydrochaeris hydrochaeris*	Capybara	Mainland
		Large BS					

Columns: Fossil species (scientific name and BM) and extant species (BM, scientific name, common name and origin). The species are ordered from small to large BM. Those from islands are in grey color. Legend: black squares indicate general rodent species, black points indicate glirid species and black stars indicate murid species. All BM information of extant species is from Mones and Ojasti (1986), Silva and Downing (1995) and Veatch et al. (2014).

(Jentink 1892) and *Phloeomys pallidus* Nehring 1890], with the exception of *Cricetomys gambianus* Waterhouse 1840, which dwells in Central-South African habitats (Tab. 10.2) (Silva and Downing 1995). In the case of glirids, the largest extant species are the fat and the garden dormouse [*Glis glis* (Linnaeus 1766) and *Eliomys quercinus* Linnaeus 1766 respectively] (Silva and Downing 1995). The extinct dormice analyzed here weigh slightly more than these two extant species (Tab. 10.2). Taking into account murids and glirids, our results suggest that the fossil insular species assessed in our research are heavier than their extant relatives (Chapter 4: Fig. 4).

At present, it is possible to define three phylogenetic groups of lagomorphs that differ in their BMs: pikas, rabbits and hares (Tab. 10.3) (Chapman and Flux 1990). The largest lagomorph species are leporids: the Artic hare, the antelope jackrabbit and the European hare (Tab. 10.3) (Silva and Downing 1995). The only extant insular species of lagomorphs are the leporids: *Nesolagus netscheri* (Schlegel 1880) and *Pentalagus furnessi* (Stone 1900) (Gorog 1999, Yamada and Cervantes 2005, Woodbury 2013). The only leporid included in our analysis, *N. rex*, is significantly greater than current species (mainland and insular). On the other hand, extant ochotonids have BMs, which are very similar among them, whereby the silver pika is considered to be the largest (Smith 1988, Silva and Downing 1995). The BMs estimated for *Prolagus* species (*P. apricenicus*, *P.* cf. *calpensis*, *P. figaro* and *P. sardus*) exceed those of silver pikas and suggest that this group holds an intermediate position between extant pikas and leporids (slightly overlapping with the smaller leporids, chapter 8: Fig. 3). Thus, they should play a distinctive role in ecosystems. In this case the insular species of lagomorphs also assessed in our research attain larger BMs than their extant relatives.

TABLE 10.3. Comparative table of the BM of the fossil lagomorph species assessed in our research and the BM of the largest extant species (excepting averages).

Fossil species				Extant species			
Scientific name	BM			BM	Scientific name	Common name	Origin
		Small BS					
			●	70-250 g	The average weight of pikas (Ochotonidae family)		
Prolagus apricenicus	282-600 g	●	●	250 g	*Ochotona argentata*	Silver pika	Mainland
Prolagus cf. calpensis	320-364 g	●					
Prolagus figaro	400-435 g	●					
Prolagus sardus	500-525 g	●					
			★	0,5-4 kg	The average weight of rabbits (Leporidae family)		
			★	1-5 kg	The average weight of hares (Leporidae family)		
			★	1.5 kg	*Nesolagus netscheri*	Sumatran rabbit	Sumatra Island
			★	2-2.5 kg	*Pentalagus furnessi*	Amami rabbit	Amami Island
			★	3-4 kg	*Lepus europaeus*	European hare	Mainland
			★	3.4 kg	*Lepus alleni*	Antelope jackrabbit	Mainland
			★	5 kg	*Lepus articus*	Artic hare	Mainland
Nuralagus rex	8 kg	★					
		Large BS					

Columns: Fossil species (scientific name and BM) and extant species (BM, scientific name, common name and origin). The species are ordered from small to large BM. Those from islands are in grey color. Legend: black points are ochotonids and black stars are leporids. All BM information of extant species is from Flux (1990), Silva and Downing (1995), and Woodbury (2013).

Finally, the soricids are also contextualized with the BM of extant species of shrews and shrew mice. The family Soricidae includes the smallest living terrestrial mammal (Etruscan shrew) with most of their species weighing between 10 and 20 g (Silva and Downing 1995, Ferry 2005). We highlight the Asian house shrew that can weigh up to 100 g (Tab. 10.4) (Silva and Downing 1995). The species from the Tribe Nectogalini are the extant relatives of *Asoriculus* Kretzoi 1959 and *Nesiotites* species (Wilson and Reeder 2005). Our results show that the fossil species are heavier than the extant ones, excepting the Asiatic water shrews (*Chimarrogale* sp. Anderson 1877, some of them from islands) (Tab. 10.4). On the other hand, the weights of the species of *Crocidura* Wagler 1832 assessed are in line with extant *Crocidura* species [excepting *C. flavescens* (Geoffroy 1827) and *C. olivieri odorata* Leconte 1857] (Tab. 10.4, see also chapter 9: Fig. 5).

Table 10.4. Comparative table of the BM of the fossil soricids species assessed in our research and the BM of the extant relative species and of the largest species.

Fossil species				Extant species			
Scientific name	BM			BM	Scientific name	Common name	Origin
		Small BS					
			■	2 g	*Suncus etruscus*	Etruscan shrew	Mainland
			★	5-9 g	*Epirsoriculus* sp.	*Episoriculus* shrew	Mainland
			★	5-15 g	*Chodsigoa* sp.	*Chodsigoa* shrews	Mainland
Crocidura kornfeldi	8.5 g	●	■	10-20 g	The average weight of soricids (including *Crocidura*)		
Crocidura sicula sicula	8.6 g	●					
Asoriculus gibberodon	8.9 g	★					
Crocidura sicula esuae	9.5 g	●					
Crocidura zimmermanni	7-10 g	●					
Nesiotites ponsi	14.6 g	★	★	13-15 g	*Neomys* sp.	Water shrews	Mainland
			●	18.5 g	*Crocidura lepidura*	Sumatran giant shrew	Sumatra
Asoriculus similis	20.4 g	★					
Nesiotites meloussae	24.8 g	★					
Asoriculus burgioi	27.5 g	★					
Nesiotites hidalgo	26-30 g	★	★	30 g	*Chimarrogale platycephalus*	Japanese water shrew	Japan Island
			★	31 g	*Chimarrogale phaeura*	Borneo water shrew	Borneo Island
			★	31 g	*Chimarrogale sumatrana*	Sumatra water shrew	Sumatra Island
			●	51 g	*Crocidura flavescens*	Greater red musk shrew	Mainland
			★	55 g	*Chimarrogale hantu*	Malayan water shrew	Malaysia
			●	60 g	*Crocidura olivieri odorata*	African giant shrew	Mainland
			■	100 g	*Suncus murinus*	Asian house shrew	Mainland
		Large BS					

Columns: Fossil species (scientific name and BM) and extant species (BM, scientific name, common name and origin). The species are ordered from small to large BM. Those from islands are in grey color. Legend: black squares indicate general soricid species, black points are *Crocidura* species and black stars species of the tribe Nectogalini. All BM information of extant species is from Silva and Downing (1995).

10.3. Body mass evolution and Island Rule in small extinct mammals

Abiotic and biotic variation in the environment (such as climatic changes or introduction into new habitats) entails a relevant and critical event for the survival of the species. At the first stage, the phenotypic plasticity of the individuals is the mechanism that allows adaptation to these new selective regimes (Strickland and Norris 2015), but later these biological changes are selected (from the genetic variation of the population, pool gene) improving the fitness of individuals and the species evolves (Stearns and Koella 1986, Keogh et al. 2005, Whitman and Agrawal 2009). Adaptation is promoted as long as selective regimes of the new and previous environment are different (Lande 2015) and is favored when there is a restricted gene flow with the original site (MacArthur and Wilson 1967, Van Buskirk and Arioli 2005). In the light of these ideas, the common biological modifications observed in insular species (morphological, demographic, behavioral, among others; see chapter 1) have to be understood as adaptations to the new insular environment (selection) (Sondaar 1977, Lomolino 2005), and not as a founder effect (reduced genetic variation) (Pergams and Ashley 2001).

Meiri et al. (2008) proposed that the evolution of BM in island extant ecosystems is a multifactorial phenomenon (Lomolino et al. 2012). It depends on: 1) the biology of the species, 2) the environment of the island, and 3) the contingency. Biologically, certain phylogenetic constraints (genetic basis) may occur and they can prevent some phenotypic changes (Whitman and Agrawal 2009) and, hence, hamper the adaptations process of the individuals. It is well established that some groups are more predisposed (pre-adapted) to a particular environmental change as a result of their particular genotype. The species assessed in this study belong to the group of small mammals, which are more often *r*-strategists. In addition to demographic and LH traits (see chapter 1), some authors described this kind of species for their better dispersal properties (introducing to new and different environments with higher probability) (Whitman and Agrawal 2009, Holling 2010). For this reason, it is proposed that plasticity may be favored in this group (Whitman and Agrawal 2009), suggesting few constraints at phylogenetic level. It is also true that traits of the behavior or locomotion of the species may also influence the degree of selective pressures of the environment. For example, species with certain lifestyles or locomotion may be less exposed to predators, and their extrinsic mortality will be lower than another. This is of particular interest in small insular mammals, where birds of prey are top predators. Some behaviors or lifestyles (e.g. fossorial) of rodents, pikas or soricids may reduce their predation levels in insular ecosystems in contrast to those of other species. In this way, these biological aspects of a species might contribute partially to the weight changes observed on islands, but it is the new environment which triggers the overall BS shift. At present, the biology (physiology, phenotypic plasticity, locomotion and behavior) of the species assessed in this study is almost unknown. Thus, we cannot address this issue satisfactorily with the current data.

As stated above, it is the new selective regime of the insular ecosystem which triggers the BS shift of new colonizers. However, as a consequence of the particularities of each islands (both geographic traits and biota), the changes do not always take the same direction and do not always have the same magnitude. Community ecologists have proposed several hypotheses to explain how ecological pressures trigger gigantism operating directly on BS of small mammals (Case 1982, Schwaner and Sarre 1988):

1) Predation hypothesis: Van Valen (1973a), Heaney (1978) and other authors (Sondaar 1977, Lawlor 1982, Maiorana 1990, Michaux et al. 2002, among others) proposed that small mammals, which escape into refuges from predators, evolve larger morphotypes because of the general absence of mammalian carnivores on islands (predation pressure release).

2) Food availability hypothesis: Foster (1964), Lomolino (1985), McNab (1994b, 2002a, 2010, 2012) and other authors (Case 1978, Heaney 1978, Lawlor 1982, among others) proposed that small mammals have an expansion of their ecological niche on islands as a result of the absence of interspecific competitors (competitive release) and, thus, they should increase BS, especially generalists and territorial species (see Case 1978, Lawlor 1982).

3) Social-sexual hypothesis: Schwaner and Sarre (1988) proposed that the high density of insular populations triggers high intraspecific competition among males and females. Selection may encourage for larger BS as a consequence of male-male combat for mates.

Lomolino's et al. (2012) study is one of the last updates on the IR field concerning extant faunas. According with this study, the main drivers of BM shift in extant insular species are: area of the island, latitude of the island, isolation from mainland, or presence of competitors or predators (factors previously considered in other studies, see Case 1978, Heaney 1978, Melton 1982, Lomolino 1985, 2005, Adler and Levins 1994, McNab 2002a, 2002b, 2010, Michaux et al. 2002, White and Searle 2007, Russell et al. 2011, among others). They also noted the role of the ancestor's BM in order to determine the direction of BM shifts. Particularly in the case of micromammals, Lomolino et al. (2012) noticed that they are strongly influenced by island area, but interpreted as a surrogate for the habitat diversity and number of predators and competitors (concerning predation and food availability hypotheses) (McNab 2002a, 2002b, Michaux et al. 2002, Russell et al. 2011,). Moreover, the study of Lomolino and collaborators (2012) also found that maximum degree of gigantism is developed in intermediate ranges of isolation and latitude (c. 40 km isolation and 50º latitude) (see also the effects of latitude in small mammals in Yom-Tov et al. 1999). Van der Geer et al. (2013) suggested that in fossil small mammals the ecological release (absence of competitors and predators) is also the mechanism for the BS shift (see also MacArthur and Wilson 1967, McNab 1994b, 2002a, 2002b). Palombo (2007, 2009a) suggested that in insular fossil communities, the BS shift of non-carnivorous mammals depends on the intra-guild competition and on the nature of species (competitive release). However, her discussion is focused basically on cases of dwarfism.

Other researchers, however, interpreted the BS shift on islands as consequence of changes in the LH (and its traits) of individuals in these new environments. One of the first in proposing this hypothesis for small mammals was Melton (1982), who studied the cricetid *Peromyscus* Gloger 1841 from the islands near British Columbia (Canada). He showed that the reduced interspecific competition and the low predation lead to higher densities in insular populations (high intraspecific competition) (see chapter 1: Fig. 1). Following MacArthur and Wilson's *r*/*K* selection theory, he suggested that selection triggers greater efficiency in resource use (*K* selection). Therefore, he proposed that as a result of these new ecological regimes, juvenile survivorship is reduced but adults live longer and produce smaller litters. In turn, and as consequence of this, it is generated a larger BS (Levins and Adler 1993, Adler and Levins 1994: Fig. 2). In later studies, it has been observed that rodents are able to modify/adjust their reproductive effort (proportion of total energy inverted in reproduction) with changes in population density (Adler and Levins 1994 and references therein). This is in accordance with *r*/*K* selection theory and LHT. To sum up, the special selective regime of islands triggers changes in demographic (density and other traits) and LH traits (reproductive effort and others), and indirectly in BS, which maximizes the individual's reproductive fitness (MacArthur and Wilson 1967, Stearns 1992). There is empirical evidence that BM in insular *Peromyscus* varies temporally, being larger when there are peak densities of the population (Adler and Levins 1994 and references therein). Based on these studies and others, Palkovacs (2003) explained gigantism on islands in small mammals as a result of a relatively stronger influence of decrease in extrinsic mortality than of resource limitation (chapter

1: Fig. 1.2). These ecological conditions select for delayed maturity at similar growth rate (Erickson et al. 2003, Orlandi-Oliveras et al. 2016) and, thus, a larger BS. Hence, small mammals develop a giant morphotype compared with its mainland ancestor. These LH changes (including BS) will improve their fitness (reproductive) in insular habitats compared with mainland strategies (evolved under high predation risk). Conversely, some authors indicated that the larger BS of giant species is achieved by an increase in the growth rate of individuals (in accordance with the food availability hypothesis) (Aubret 2012, Gray et al. 2015) or a mix between extended longevity and high growth rate (Herczeg et al. 2009). Palkovacs (2003) also proposed that resource limitation (that affects growth rate) and lower extrinsic mortality (that affects the reaction norm) may act together (see chapter 1: Fig. 1). For example, insular species of *Anolis* (Daudin 1802) have a larger BS due to a reduction in growth rate (a minimal resource limitation, change in growth rate) and delayed maturity (important low extrinsic mortality, change in reaction norm) (Case 1978).

Direction and magnitude of body size shift in extinct insular small mammals

To achieve the goals of this study, it is essential to compare the BMs among mainland ancestors and insular descendants (Adler and Levins 1994, Table 10.5 and Fig. 10.1). This provides information about direction and magnitude of BM shifts on islands.

Because of the morphological adaptations to insular ecosystems and the bias of the fossil record, the ancestor of most of the insular species is often unknown or uncertain. This is the case of: *A. burgioi*, *C. bravoi*, *C. tamarani*, *M. magna*, *M. cyclopeus*, *N. rex* and *P. apricenicus* (Quintana et al. 2011, Michaux et al. 2012, Masini et al. 2013, 2014, Quintana 2014). In other cases, the remains of the ancestor are scarce or poorly studied, and BM approximations are not possible (Tab. 10.5). For example: 1) *P. figaro and P. sardus* are the descendent lineage of *P. sorbinii* Masini 1989 of which mainly teeth are preserved (Angelone et al. 2015); 2) the postcranial of the ancestor the *Hypnomys* lineage (*Eliomys truci* Mein and Michaux 1970) is not well-studied (Bover et al. 2010b); 3) the ancestor of *C. sicula* subsp. (Miller 1901) may be an unknown common ancestor of both *Crocidura tarfayensis* Vesmanis and Vesmanis 1980 and *Crocidura canariensis* Hutterer, López-Jurado and Vogel 1987 (Dubey et al. 2008). The forerunner is reliably identified only in some of the soricid species assessed: *C. kornfeldi* is the ancestor of *C. zimmermanni*, and *A. gibberodon* of *A. similis* and the *Nesiotites* lineage (Kotsakis 1980, Reumer 1986, Made 1999, Rofes et al. 2012). Our results show that *A. similis* and *Nesiotites* sp. are significantly larger than their ancestor, but BMs of *C. kornfeldi* and *C. zimmermanni* remained similar and without differences (Tab. 10.5, Fig. 10.1, see also chapter 9: Tab. 5). The first two species can be considered as genuine insular giants.

The large size (BM) of some of the other insular species analyzed (*A. burgioi*, *C. bravoi*, *C. tamarani*, *H. morpheus*, *H. onicensis*, *M. magna*, *N. rex*, *P. apricenicus*) in comparison with the extant fauna (see section 10.2) also suggests gigantism. It is also of interest to compare related species from islands (I) and mainland (M) for determining BS shifts (gigantism) in absence of the true ancestor: *A. burgioi* (I) and *A. gibberodon* (M), *C. sicula* subsp. (I) and *C. kornfeldi* (M), and *Prolagus* species from Gargano and Sardinia (I) and *P.* cf. *calpensis* (M) (Tab. 10.5). The soricid *A. burgioi* shows significant differences with the mainland species, but this is not the case of the subspecies of *C. sicula* (Tab. 10.5). This observation follows the same pattern as *Nestioties*, *A. similis*, and *C. zimmermanni*. In lagomorphs, we observe that the youngest population of *P. apricenicus* (fissure filling F8; BM=600 g) and the populations of *P. figaro* and *P. sardus* are larger than the mainland forms. However, this is not the case of the oldest population (fissure filling F1) of *P. apricenicus* (BM=282.2 g) (Tab. 10.5).

Table 10.5. BM (in g) of the species assessed in our research in comparison to the BM of their mainland ancestors or extant relatives.

Mainland ancestor		Extant relative		Insular descendent	
Species	BM	Species	BM	Species	BM
ORDER RODENTIA					
?	?	*Pelomys fallax*	130	*Canariomys bravoi*	1571.3
		Arvicanthis niloticus	75	*Canariomys tamarani*	1010.7
Eliomys truci	?	*Eliomys quercinus*	90	*Hypnomys morpheus*	232.7
		Eliomys melanurus	75	*Hypnomys onicensis*	201.5
Murinae nov. gen. et sp.	?	?	?	*Mikrotia magna*	1300-1900
(?) *Muscardinus vireti*	?	*Muscardinus avellanarius*	22	*Muscardinus cyclopeus*	101.7
ORDER LAGOMORPHA					
Prolagus oeningensis-like	?	Ochotonids	70 -250 g	*Prolagus apricenicus*	282.2-600
Prolagus sorbinii	?			*Prolagus figaro*	400-435
				Prolagus sardus	500-525
Prolagus cf. *calpensis*	320-360			-	-
?	?	?	?	*Nuralagus rex*	8241.5
FAMILY SORICIDAE					
Asoriculus gibberodon	8.9	?	?	*Asoriculus similis*	20.4
				Nesiotites ponsi	14.6
				Nesiotites meloussae	24.8
				Nesiotites hidalgo	26-30
Crocidura kornfeldi	8.5	?	?	*Crocidura zimmermanni*	7-10
?	?	?	?	*Asoriculus burgioi*	27.5
(?) *Crocidura tarfayensis*	?	?	?	*Crocidura sicula esuae*	9.5
				Crocidura sicula sícula	8.6

Columns: Mainland ancestor (species and BM), extant relative (species and BM) and insular descendent (species and BM). The chart is split by order or family. Symbol "?" indicates that the ancestor, mainland relative and/or BM of that species is not known. Symbol "-" indicates that there is no evidence that it was the ancestor of an insular species. Solid lines separate different species, dotted lines separate anagenetic species or species with the same ancestor, and dashed line separate extant relative species. BM information of extant species is from Silva and Downing (1995).

Undoubtedly, we are not observing a case of dwarfism in pikas. Probably the mainland ancestor was a pre-Messinian medium-sized species smaller than *P.* cf. *calpensis*, as suggested by the taxonomical studies of Angelone (2007) and Angelone and Čermák (2015).

Factors that trigger the Island Rule in small mammals: a paleontological view

As discussed above, the main ecological drivers of BM shifts in extant insular species here proposed are: area of the island, latitude of the island, isolation from mainland, and presence of competitors or predators. Lomolino et al. (2012) considered these ecological characteristics as indicators of the selective pressures that operate directly on BS (see Predation and Food availability hypotheses). On the other hand, these ecological characteristics also modified directly the levels of extrinsic mortality and resource availability of the islands (area and climate determine resources, and area and isolation determine the number of predators and competitors of the island), which modulated the LH of species (and indirectly the BS) following the model of Palkovacs (2003). From a paleontological point of view, environmental changes (e.g. climatic) must be taken into special consideration because they modify the ecological main drivers: 1) number of competitors and predators (a change that affects the faunal composition, e.g. new arrivals of species from the mainland), 2) the conformation of the island: area and isolation (e.g. sea level changes), or/and 3) productivity (resources). Our results attempt to show which environmental characteristics may explain the BS shifts of small extinct mammals in insular environments (Mediterranean Islands).

In chapter 9, we assess the gigantism of shrews from several islands, and observe that some of them cannot be considered giants: BM of *C. zimmermanni* (from Crete) is not different from that of ancestor, while *Nesiotites* and *A. similis* (from Mallorca and Sardinia respectively) are considered as true giants (Fig. 10.1). Following the statements of previous paragraph, we have decided to address this observation (absence or presence of gigantism) through the assessment of the ecological features of their respective islands (this information is summarized in chapter 9: Tab. 6). Two main differences are observed: 1) the size of the island and 2) the distance island-mainland (degree of isolation). Previous studies of gigantism (and other traits of the IS) in extant small mammals also underlined the importance of these two factors (Foster 1964, Heaney 1978, Gliwicz 1980, Adler and Levins 1994, Hasegawa 1994, Lomolino et al. 2012, among others), and particularly White and Searle (2007) suggested these forces to be the triggers of gigantism in insular populations of common shrew (*Sorex araneus* Linnaeus 1758) from the Scottish Islands. In respect to island area, Mallorca and Sardinia are the smallest and largest islands, indicating that the dimensions of Crete (e.g. food availability) are not among the factors that precluded the increment in BS of the Cretan shrew species. In respect to the isolation, its magnitude is not only measured by the distance, but also by the nature of the barrier and the difficulty of crossing it (Adler and Levins 1994). Accordingly, the two former islands are more isolated from the mainland with deep and wide barriers of sea (Marra 2005), while Crete is closer to the mainland (narrow sea), and an archipelago was present between Crete and the mainland (Marra 2005). The isolation of islands is very important because the immigration rate depends on it and, consequently, the entrance of mainland fauna too (MacArthur and Wilson 1967). Adler et al. (1986) observed that the insular populations of white-footed mouse [*Peromyscus leucopus* (Rafinesque 1818)] that inhabit islands close to the mainland have demographic traits similar to the mainland species (lower population densities). These nearby islands were not continuously surrounded by water, and the mice could move between them. The most isolated ones show the expected IS (reduced dispersal, see Tamarin 1978). Thus, the proximity to mainland combined with the easy access (archipelago) of Crete suggest that the probability of immigration events is higher than in Mallorca and Sardinia. This suggests greater presence of competitors and predators from the mainland on the one hand and dispersal sinks (zones of gene flow) in these insular shrew populations. This, combined with the fact that the major consumers of shrews on the mainland are birds of prey (Korpimäki and Norrdahl 1989), leads us to propose that Cretian shrews had: 1) an elevate number of predators (Predation hypothesis, they have to escape from them) and, hence, 2) high extrinsic mortality (Palkovacs 2003). This factor clearly precludes a BM shift towards gigantism in *C. zimermanni*. Taking into account the comparison between insular and mainland species performed in the previous section, we also identified *C. sicula* subsp. (from Sicily) as not gigantic (Fig. 10.1). Sicily was also poorly separated from the mainland, and an archipelago was situated between this island and the mainland during the period of *C. sicula* subsp. (Marra 2005). This latter observation reinforces our hypothesis and lends

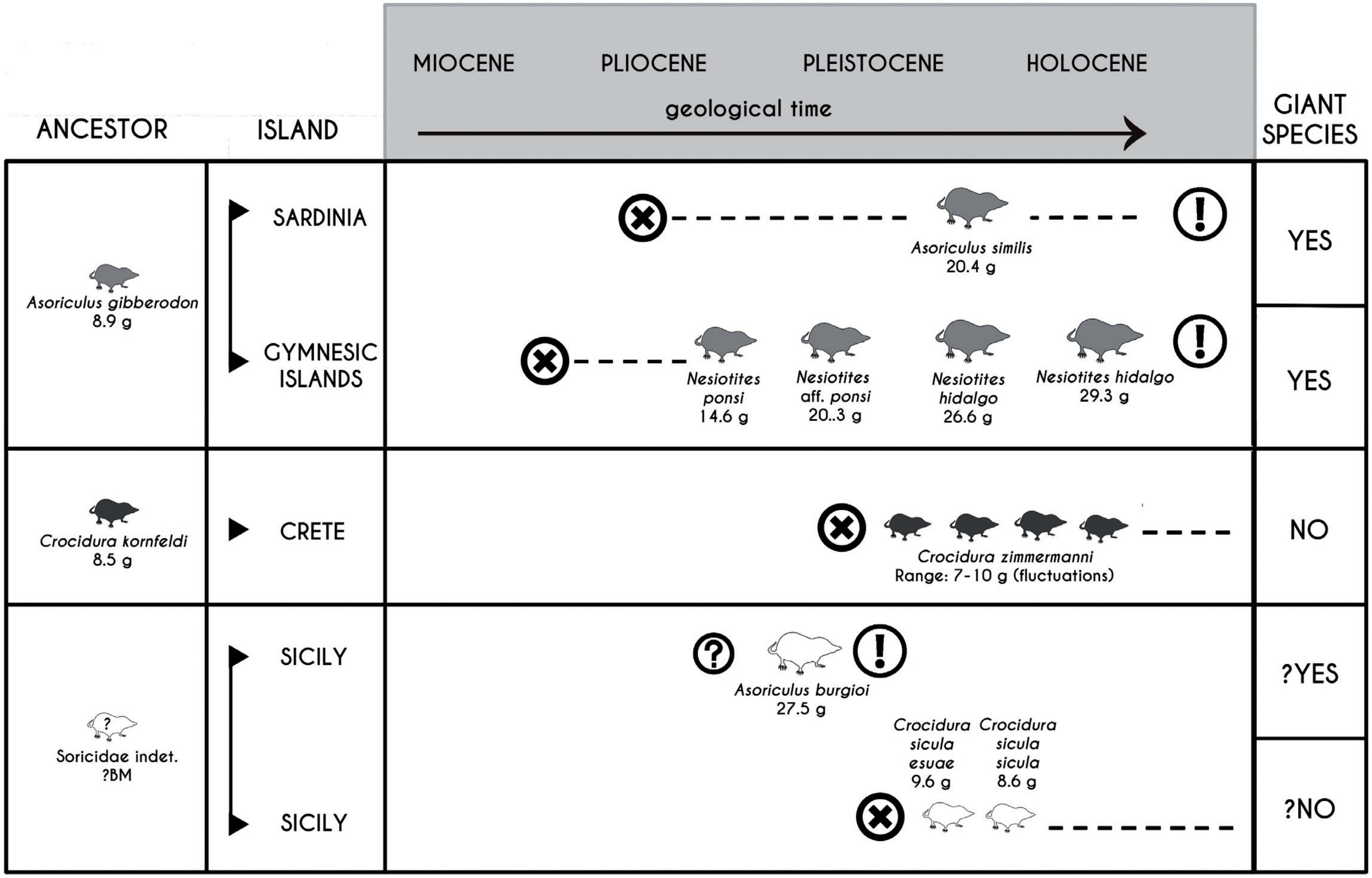

FIGURE 10.1. Diagram of the soricid species assessed in our research from some Mediterranean Islands and their mainland ancestors, in order to see the BS changes ancestor-descendent and among several populations of one species (or anagenetic species). The size of the silhouettes is indicative of the BS of the species. Symbols: Circled X (ancestor's arrival); circled "?" (unknown age of ancestor's arrival); circled "!" (extinction of the species); and dashed lines (presence of the species on the island). Column "giant species": Yes, No, "?Yes" or "?No" (? symbol indicates that it is probable that this species was (or not) giant, but the ancestor of it is unknown), following comparisons with BM of the ancestor (see the text).

support to the notion that the degree of isolation was an important factor conditioning BM of shrews, and probably also that of other small mammals. The importance of predators has been highlighted in several studies of extant insular giants (see Adler and Levins 1994, Hasegawa 1994, Michaux et al. 2002 and references therein). Van den Hoek Ostende et al. (2014) underlined the lack of spectacular gigantism and adaptive speciation in the Cretian rodents, but they proposed that climatic factors and biological constraints (mainly phylogeny) are the factors responsible for this absence. Considering the absence of gigantism pattern in Cretian micromammals as a whole, a biological (phylogenetic) explanation (concerning several species of different orders) seems little credible while the ecological factors (isolation) as modifiers of the insular regimes are more supported. Our explanation lends support to the notion of the absence of spectacular gigantism in Cretian rodents; nevertheless, it must previously be confirmed that these rodents were not giants through a reliable a BS assessment as Van den Hoek Ostende et al. (2014) pointed out.

In chapter 7, we have assessed the changes in BM of two anagenetic species of *Prolagus* from the island of Sardinia. The evolutionary step from *P. figaro* to *P. sardus* seems to be related with a climatic change that took place during the mid-Pleistocene transition and that caused the highest species turnover in the Quaternary of Sardinia (extinction of some species and anagenetic evolution of others) (Palombo 2009b, Pascucci et al. 2014, see also chapter 3). Other authors suggested that Sardinian insular species at that time had either to adapt to the new environment by certain modifications (including BS shifts) or went extinct (Abbazzi et al. 2004). The mid-Pleistocene climate change was characterized by strong temperature fluctuations (following BR, Boldrini and Palombo 2010) and led to a total reorganization of the insular habitat of Sardinia (extinction of some species and anagenetic evolution of others). Hence, it is as if we have been assessing two different islands (prior and after climatic change). The results presented in chapter 7 indicated that *P. sardus* was characterized by a significant larger BM than *P. figaro* (ca 50-100 g) (tachytelic stage), besides dental and other morphological modifications. Hence, we may deduce that this climatic change triggered a different environment in Sardinia (predators, competitors, resources, among other traits) that led to a shift in BM between the two anagenetic species. From Orosei 2 Subcomplex to Dragonara Subcomplex (prior and after the climatic change), the terrestrial predators were reduced (not taking into account the otters, which feed on marine resources) (see chapter 3). This change in the number of predators may be one of the factors that triggered a large BS in *P. sardus*. This is in agreement with our results from shrews and extant studies of gigantism (see previous references above).

The FCs of Sardinia are practically the only ones of the Mediterranean Sea (excepting Sicily) that have carnivorous species [*Chasmaporthetes* Hay 1921, *Mustela* Linnaeus 1758, *Pannonictis* Kormos 1931, *Cynotherium sardous* Studiati 1857] (Palombo 2007, Masini et al. 2008, Lyras et al. 2010; see chapter 3). This is a consequence of its large area (Heaney 1984). Taking into account the impact of predators observed in our shrew study (chapter 9) and studies of extant fauna, the coexistence of *Prolagus* lineage (*P. figaro* and *P. sardus*) with carnivorous species may indicate a mainland-like ecosystem, and consequently, an absence of BS change (as in *C. zimmermanni*) (Adler and Levins 1994, Russell et al. 2011). As previously stated, however, BM within the *Prolagus* lineage is larger than that of *P.* cf. *calpensis*, a mainland dweller (although this is not the direct ancestor), and BM increased within the two anagenetic species. This increase of BM in the presence of carnivores may be explained by several factors:

1) Firstly, these carnivores did not exert an important predation pressure on the *Prolagus* lineage. They predators were composed of canids, mustelids and hyaenids, whose extant

representatives are considered hunters, scavengers or opportunistic feeders. One of the most studied is the endemic *Cynotherium sardous*. Although originally it was described as a specialized *Prolagus* hunter (Malatesta 1970), recent studies considered it as a small-prey hunter (possibly small mammals and birds, among others), but without any evidence that its food source is exclusively *Prolagus* individuals (Lyras and Van der Geer 2006, Lyras et al. 2006, 2010). Other small mammals of Sardinia (three species of rodents, one mole, one shrew and one leporid, in Orosei 2 subcomplex; see chapter 3) could also have been a food source for these carnivorous species. Therefore, and because of the low number of carnivores in comparison with the mainland, we suggested that predation pressure was lower in Sardinia than on the mainland.

2) Secondly, another hypothesis suggests the co-evolution of predator and prey species. Following Van Valen's theory (1973b), predator and prey species improve their skills (capture/escape) over evolutionary time while maintaining the same fitness due to their coevolution. Lyras et al. (2006) suggested a size reduction of *Cynotherium* Studiati 1857 comparing material from different sites ordered chronologically. However, the increase in BM of *Prolagus* comprises periods with different species of predators (not only *Cynotherium*, see chapter 3), and, hence, the conditions do not apply here.

When the BMs of Sardinian *Prolagus* (chapter 7) are compared with the Apulian *P. apricenicus* (chapter 6), it is observed that BM increase in the latter species is greater than in the former (ca. 100 g more, Tab. 10.5). While Sardinian *Prolagus* coexisted with several species of carnivores, *P. apricenicus* inhabited an island full of micromammals (resource limitation) with fewer predators (low predation pressure). Hence, the smaller BM of Sardinian *Prolagus* (ca. 100 g less) can be explained as a consequence of their coexistence with several mammalian carnivores. However, see below for the complexity of the fauna of Gargano paleo-island.

The previous results lend support to the notion that predators play an important role in the gigantism of small mammals (IR). These previous studies (chapter 7 and 9) only deal with continental or oceanic-like islands which are close to the mainland and are, hence, more susceptible to biota renovations. We are also interested in ecosystem free of terrestrial carnivores (oceanic islands). For this purpose, in chapter 4 we assess the BM of the two Canarian murid species: *C. bravoi* (1500 g, Tenerife) is larger than *C. tamarani* (1000 g, Gran Canaria). Both species lived in very similar ecosystems (isolation, latitude and climate) with lizards and birds of prey, none of which specialized in their consumption (Rando 2003, Sánchez Marco 2010). Moreover, it is also likely that these murids share the same ancestor. The only feature that distinguishes them is the island area that they inhabited (current extension): 2034 km^2 of Tenerife (*C. bravoi*) and 1560 km^2 of Gran Canaria (*C. tamarani*) (Instituto Geográfico Nacional 2016). Hence, the results of chapter 4 suggest that island area of island (resources) can play an important role in insular gigantism under absence of predators (oceanic islands). The importance of island area as an important driver have also been observed in the study of Heaney (1978), who assessed the Asian tri-colored squirrel [*Callosciurus prevostii* (Desmarest 1822)] from several islands of Malaysia and Indonesia. All squirrel populations (subspecies) live in similar ecosystems (latitude, climate, predators and competitors) and the only difference is in the island area and the degree of isolation. Accordingly, Heaney observed that BS of squirrels increases gradually with island area to a maximum (island area of 10000 km^2) from which the BS begins to decrease. On the other hand, Lawlor (1982) proposed that small mammals that are specialist feeders experience a larger resource limitation than generalists on islands. Therefore, specialist species do not evolve towards large giant morphtypes. In several occasions, species of smaller size than their ancestor (dwarf rodents) have evolved on islands (Durst and Roth 2015). The results from our C*anariomys* study highlight the important role of resources availability in small mammals when predation is minimal. The island area of *C. tamarani* was smaller than that of *C. bravoi* and, hence, *C. tamarani* suffered greater resource limitation. This, at last instance, implies that the large BS of species from larger islands cannot be achieved on smaller islands. Thus, we conclude that resource availability has an important effect on BS in small mammals, limiting the maximum attainable BS (because it limits the maximum growth rate, GR, in accordance with Palkovacs 2003).

Finally in chapter 5 we have studied the very complex insular biota of Gargano. It is considered complex not only because of the endemic fauna, but also because the island was submerged during the Early Pleistocene and later emerged connected to the mainland. Although terrestrial predators are only represented by crocodiles and snakes (few predator species) and macromammals are scarce, the FC of Gargano is full of micromammals (Masini et al. 2010, see chapter 3). In this case, neither and estimation of the island area nor the degree of isolation of the paleo-island from the mainland or from other islands is possible. We estimated the weight of the murid *Mikrotia magna* and obtained values similar to those of *C. bravoi* (1300-1900 g and 1500 g respectively). Taking into account the aforementioned problems and the insights from studies of extant fauna (Hasegawa 1994, Russell et al. 2011, among others), it is striking that *M. magna* could achieve a similar BM as a species that lived in a competitor-free environment (*M. magna* and *C. bravoi* lived in a habitat with few predators). The most important competitors of *Mikrotia* were *Prolagus* (grassland dwellers), cricetids (burrowers) and other species of *Mikrotia* (De Giuli et al. 1987, Parra et al. 1999). Thus, *Mikrotia* genus experienced high interspecific competition on the Gargano paleo-island. As stated above, resource limitations are also important in determining the maximum BS that can be achieved. We do not know the area of Gargano, but the presence of a large number of competitors must have importantly reduced the resource pool; hence, it is unexpected that *M. magna* could develop such a large BM on the Gargano paleo-island. We suggest that it is likely that another habitat was the origin of *M. magna*. Our suggestion is in agreement with previous geological and paleontological studies (Abbazzi et al. 1996, De Giuli and Torre 1984, De Giuli et al. 1985, Masini et al. 2008, 2010). These authors noticed that *M. magna* appeared suddenly in the fossil record (without an ancestor lineage) and proposed that this species arrived to Gargano “jumping” from a neighboring island. An ancestor of *M. magna* that was larger than the other two lineages of *Mikrotia* from Gargano can be ruled out (Masini et al. 2013, 2014). Therefore, we propose that the impressive giant morphotype of *M. magna* evolved in a different ecological habitat: an island with absence of predators and low competition. Geological and paleontological studies also suggested that the largest of the giant species of small mammals from Gargano (*Prolagus imperialis* and *Stertomys laticrestatus* Daams and Freudenthal 1985) also arrived “jumping” from another neighboring island, lending support to the notion that the high inter-guild competition of Gargano checked evolution of giant sizes.

To sum up, each island is a particular laboratory and, consequently, the patterns of gigantism (magnitude) are specific. Gigantism (IR) assessed here for extinct small mammals from Mediterranean Islands are in line with the studies of extant faunas (Lomolino 2005, Lomolino et al. 2012, and references therein). We observed that ecological factors are the main drivers of BM shift in insular environments. In the case of the extinct small mammals assessed in this research, the absence of predation is the primary driver of BS evolution in insular regimes. Under presence of predators, the expression of gigantism can be lesser (e.g. Sardinian *Prolagus*) or absent (e.g. Cretian shrews). A higher number of predators occurred in larger and closer (to the mainland) islands (see previous examples). On oceanic islands or islands with few predators, we propose that resource availability (area of the island and competition) plays a role limiting the maximum BS that a species can attain (e.g. *Canariomys* and *Mikrotia*). Our results in extinct populations are in agreement with the model of Palkovacs (2003) and the empirical evidences of other authors (Norrdahl and Korpimäki 1993, Adler and Levins 1994). They suggested that predation is the most powerful force in most rodent population (over interspecific competition) and especially in communities of only few species and low competitiveness among them. On the other hand, we should not forget the biological role (e. g. lifestyle), which can modulate the selective regimes of the species.

Evolutionary trends in body size shifts under insular regimes in extinct small mammals

Another approach to the evolution of BS on islands consists in comparing the BM of several populations or taxa forming an anagenetic lineage (Fig. 10.2). Our results indicated a trend of BM increase (no fluctuations) in small mammals over evolution: *H. onicensis* and *H. morpheus*, *N. ponsi* and *N. hidalgo*, *P. apricenicus*, *P. figaro* from different sites, and *P. sardus* from different sites, with the exception of *M. magna* (the BM increase is not statistically significant) and *C. zimmermanni* (see chapters 5 and 9 respectively) (Fig. 10.2). BS change is one of the first adaptations of insular dwellers following the colonization process (Mein 1983, Millien 2006). Some authors considered that insular populations achieve a demographic equilibrium with a subsequent period of morphological stasis (Mein 1983, Sondaar 2000, Millien 2006, Nagorsen and Cardini 2009, Cucchi et al. 2014, Aubret 2015). Our results disagree with this statement. Van der Geer et al. (2010) indicated a progressive BS increase in the *Nesiotites* lineage and a constant BS in the Cretan shrew (*C. zimmermanni*) over evolutionary time. Later, Van der Geer et al. (2013) emphasized (contradictorily) that BS of insular small mammals fluctuates without any simultaneous change in their FC (*Mus minotaurus* Bate 1942, *C. zimmermanni*, *Kritimys*, *P. sardus*, *Mikrotia*, *Hattomys* Freudenthal 1985 and *Nesiotites*), but they did not mention any pattern of BS increase.

Several abiotic factors of the environment (the Court Jester model) (Barnosky 1999, 2001), such as climatic oscillations, may explain the BM variations observed over time in our research (Alcover et al. 1981, Millien and Damuth 2004, Boldrini and Palombo 2010, Van der Geer et al. 2013). Warming is expected to trigger smaller BS (following BR) and reverse the gigantism trend (Van de Geer et al. 2013). However, these abiotic modifications are likely to lead to fluctuations of BM over time (Boldrini and Palombo 2010), while in our case a clear pattern of increase is observed (Fig. 10.2). On the other hand, following the Red Queen hypothesis, biotic interactions (e. g. predation, intra- or interspecific competition) are also proposed as important drivers of evolution (Van Valen 1973b, Benton 2009, Brockhurst et al. 2014). Following Red Queen hypothesis, species in a fast changing biotic environment are continually adapting to adaptive modifications of the other (each species' adaptation is followed by counter-adaptation in the interacting species: competitors or predators), but their average relative fitness remains constant and also the probability of extinction. As previously said, insular populations are exposed to a strong intraspecific competition (chapter 1: Fig. 1.1). Such selective regimes may explain the continuous increase in BS over time, even though the most important BS shift appears following colonization because of environmental modification (abiotic and biotic factors). The Red Queen hypothesis has been suggested to explain morphological changes in insular dwellers throughout evolution. Casanovas-Vilar et al. (2011) proposed that density-dependent selective regimes with high intraspecific competition (islands) trigger selection for high-crowned teeth coupled with other adaptations that promote their durability and efficiency in murids from the Tusco–Sardinian paleobioprovince, independently of environmental changes. Thus, the time of isolation (evolution) is another factor to take into account in analyses of BS shift in islands.

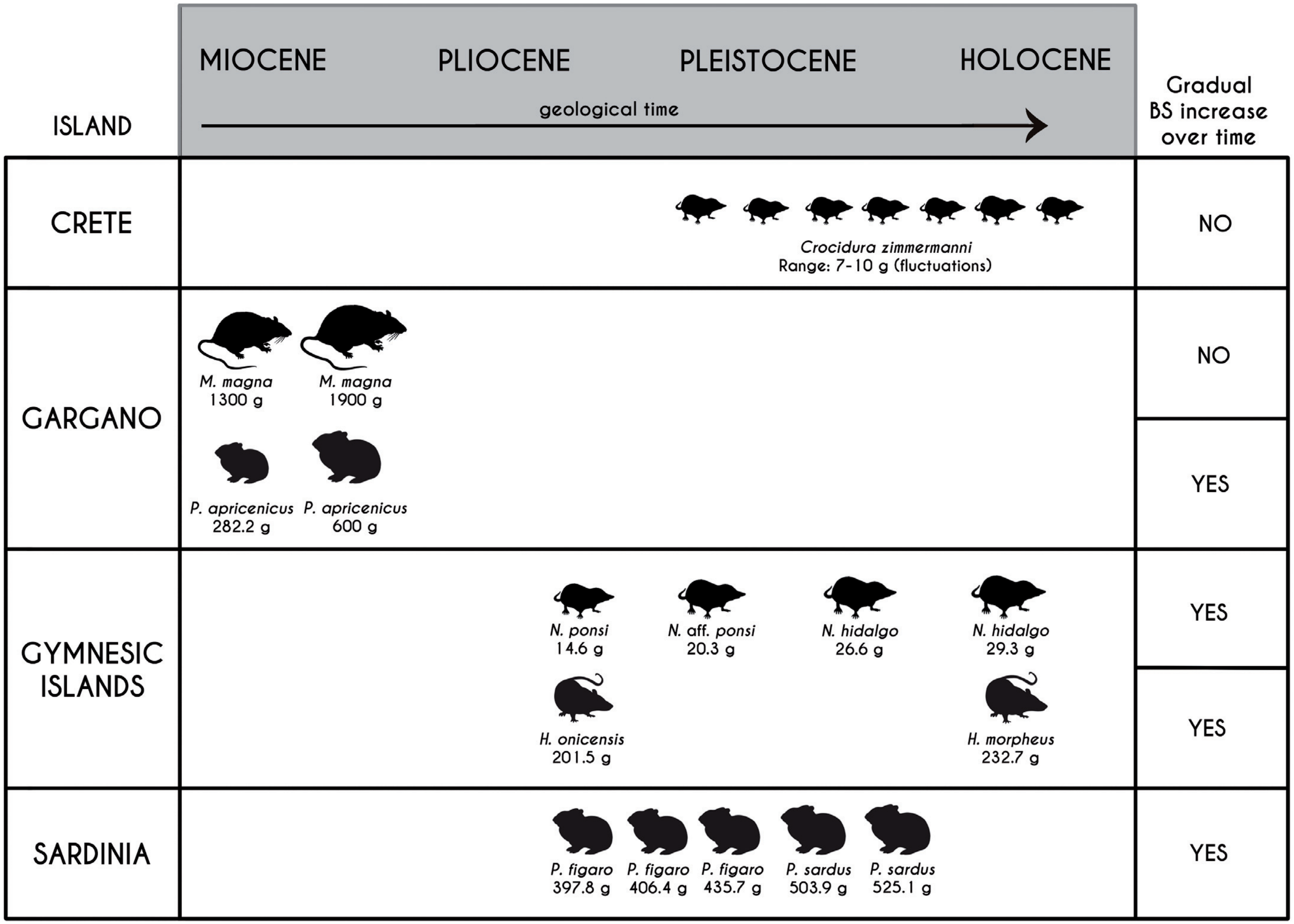

Figure 10.2. Diagram of populations ordered chronologically of some small mammals from several Mediterranean Islands assessed in our research. This diagram allows us to observe the fluctuations of BS over evolutionary time. Silhouettes represent the type of small mammals (shrew, rat, pika or rodent), below the scientific name and BM. The size of silhouettes is indicative of the BS of the species and, hence, of the BS change (interspecific comparisons of size of silhouette are only possible if they belong to the same type of small mammal). Column “gradual increase over time”: Yes or No.

Body size shifts and Life History strategy in extinct small mammals

In order to delve more deeply into the biology (certain physiological and LH traits) of fossil species, the microscopic structures of their hard tissues are studied: teeth and bones (paleohistology) (Klevezal 1996, Chinsamy-Turan 2005, Bromage et al. 2009, Padian and Lamm 2013). These kinds of analyses are widely used in fossil ectotherms (reptiles and dinosaurs) (Chinsamy-Turan 2005, Padian and Lamm 2013, and references therein), but the studies of fossil mammals (endotherms) have only recently been initiated (Bromage et al. 2002, Köhler and Moyà-Solà 2009, Köhler 2010, Jordana and Köhler 2011, Marín-Moratalla et al. 2011, Köhler et al. 2012, Orlandi-Oliveras et al. 2016, among others). We decide to analyze the microstructure of femora of *P. apricenicus* (F1 fissure filling of Gargano paleo-island), in order to reconstruct some LH traits. Principally, we focus on longevity, because in small mammals the different life stages are completed before the first year and they are not recorded in bone tissue (García-Martínez et al. 2011). A minimum longevity of 7 years was estimated for the F1 population of *P. apricenicus* (BM of 280 g).

If we look at the LH of extant pikas (the extant relatives of the genus *Prolagus*), two strategies are described depending on the habitat of the species: 1) of rocky zones and 2) of meadow zones (Smith 1988). Both groups are characterized by a similar BM, but by different LH traits. The main differences are found in longevity, age at sexual maturity, weaning age, litter size and number of litters (chapter 8: Tab. 3). The rocky pikas live longer, attain sexual maturity later, wean their offspring later, have less neonates per litter, and have smaller number of litters per year (than meadow pikas). In other words, taking the allometry into account, rocky pikas shifted towards a slow LH and meadow pikas towards a fast LH. The differences in the strategy adopted depend on the levels of extrinsic mortality of the two habitats where they live: rocky species have a low and meadow species a high average annual mortality (Smith 1988, Stearns 1992). The insular habitats are characterized by scarce presence or even by absence of terrestrial carnivores. Thus, as stated in chapter 1 (Fig. 1.1 and 1.2), it would be expected that *P. apricenicus* was affected by reduced extrinsic mortality. Similarly to extant rocky pikas (e.g. *Ochotona princeps* Richardson 1828 has a longevity of 6 years), the longevity of *P. apricenicus* estimated using histology (7 years) is higher than the value predicted by allometry (4.5 years). Following a parallel trend as extant rocky pikas, *P. apricenicus* likely moved towards a slower LH than expected from its BS. The extended longevity of this species was most likely associated with other LH changes, such as late age at maturity, small litter size or late age at weaning.

This research is one of the first dealing with LH of insular extinct small mammals (see Orlandi-Oliveras et al. 2016, or paleohistological descriptions at Kolb et al. 2015,). Extant species of pikas are absent in island ecosystems, and the biology of insular endemic leporids in natural habitats is little known: *N. netscheri* (Sumatra Island) and *P. furnessi* (Amami Island) (Gorog 1999, Woodbury 2013, see Tab. 10.3). Our results of *P. apricenicus* suggest that pikas and, more generally, small mammal species that inhabit islands move towards a slow LH (implying a longer lifespan and a later onset of reproduction time). They become species more efficient in resource acquirement and more competitive (*K*-species), and less productive species (*r*-species), in accordance with the theory of MacArthur and Wilson (1967) and the model proposed by Palkovacs (2003).

The results of our research in pristine natural habitats unaltered by human presence are in agreement with (and reinforce) previous studies (genetic or morphological) of current species of insular giants (small organisms such as birds, amphibians, mammals, among others). In the case of birds, Covas (2012) observed that insular populations have a reduced fecundity, longer developmental periods and an increased investment in young individuals. These authors suggested an interaction of insularity and latitude in other biological traits (see also reference therein, Blondel et al. 1993, Blondel 2000). In respect to amphibians, Wang et al. (2009) observed that the insular dark-spotted frog [*Rana nigromaculata* (Hallowell 1861)] allocated less energy to reproduction, produced larger eggs and had smaller clutch sizes (see other amphibian studies in Alcover et al. 1984, Li et al. 2010, Piña Fernández 2014). In the case of mammals, Austad (1993) described that the insular population of opossums from Sapelo Island [*Didelphis virginiana* (Kerr 1792)] live longer and have smaller litter size than mainland populations. Fons et al. (1997) reported a significant BS increase in shrews [*Crocidura suaveolens* (Pallas 1811)] from Corsica associated with a decrease in litter size and an increased BS of pups at birth. In other words, this Corsican shrew species allocates less energy to gestation (reproduction). Adler and Levis (1994) synthesized all the available information from the literature concerning island rodent populations. They observed that rodents respond to insular habitats with reduced reproductive outputs, greater BS and reduced aggressiveness. Several other studies on rodents are interesting: Gliwicz (1980) pointed out that insular rodent populations attain and maintain high densities and decrease their reproduction; Salvador and Fernandez (2008b) indicated for the endemic cavy (*Cavia intermedia* Cherem, Olimpio and Ximénez 1999) from Moleques do Sul Island smaller litter sizes, heavier offspring and later age at maturity than congeneric mainland species; Mappes et al. (2008) studying insular populations of the bank vole [*Myodes glareolus* (Schreber 1780)] suggested that the high intraspecific competition fosters larger offspring size, and, at last instance, lead to lower reproductive effort; several other studies report the larger BS of insular populations of small mammals and their higher densities in comparison with mainland populations (see Salvador and Fernandez 2008a, Russell et al. 2011, Crespin et al. 2012, among others). In order to further validate our results, it would be interesting to study a complete insular population of extinct small mammals and to calculate densities and some LH traits.

On the other hand, our results also evidence that in insular habitats the relationship between LH traits and BM is not that expected from allometry of typical mainland species (Köhler 2010, Healy et al. 2014: Fig. 1). We observe a decoupling among LH traits and BM in small insular mammals: our paleohistological analysis provides evidence that *P. apricenicus* is 2-3 years more long-lived than predicted from BM. This decoupling in insular small mammal populations (extinct and extant) emphasizes that LH traits are not a coevolved trait assemblage that changes as a whole (Stearns 1976). Promislow and Harvey (1990) pointed out that in mammals the best proxy of LH traits is mortality and not BS (see also Stearns 1976, 1977, 1992, Roff 2002). In species with high rates of extrinsic mortality (e.g. most mainland populations), individuals respond by increasing fecundity; while in the cases where extrinsic mortality is low (e.g. islands), the individuals decrease their fecundity. Another type of decoupling observed in insular small mammals (bats, rodents and shrews) is between metabolism and BM (McNab and Bonaccoroso 2001, Mathias et al. 2004, Magnanou et al. 2005). Thus, larger insular populations have a total energy consumption that does not differ significantly from that of smaller individuals from the continent. In other words, individuals from insular populations have a lower BMR than expected from their BM.

In the light of our results and those from studies of extant fauna, it is clear that insular dwarf mammals are not simple allometric reductions of their large mainland relatives. Nevertheless, based on this allometric point of view, several authors suggested a faster LH for insular dwarfs due to the decrease in BS (Raia et al. 2003, Raia and Meiri 2006, Palombo 2007, Meiri and Raia 2010, Larramendi and Palombo 2015). Following *r*/*K* selection and LHT, however, others proposed that large insular mammals moved towards a slow LH strategy considering the redirection of energy to growth and maintenance (MacArthur and Wilson 1967, Palkovacs 2003, Köhler and Moyà-Solà 2009, Köhler 2010, Jordana and Köhler 2011, Jordana et al. 2012).

As stated above, the BS shifts (dwarfism and gigantism) of insular mammals have been explained from two points of view. Firstly, community ecologists proposed that BS (or BM) is modified directly by selective pressures of the new insular environment (the hypothesis of predation, food availability and social-sexual behavior, see above in this section). On the other hand, Palkovacs (2003) proposed a theoretical model based on the *r*/*K* theory and LHT. In this view, the shifts of BM of insular mammals are a consequence of the modification of LH to the new environment (indirect effect). The results of this PhD Thesis (applying paleohistological techniques as well as concepts of the LHT) supports the Palkovacs (2003) view. Insular extinct small mammals analysed showed a modification of LH towards the slower end (longer longevity, even more than expected allometrically) and an increase of BM. This combined pattern is consistent with the predictions done by theoretical model of Palkovacs (2003), taking into account the decreased extrinsic mortality as the primary driver in the evolution of insular BS shift (see Fig. 1.2. Small mammals). Thus, our results clearly suggest that insular small mammal species achieve a larger BM as a consequence of the modification of their LH (towards a slower endpoint), and not as a direct effect of the selective pressures of insular environments (e.g. larger BM because they do not need to hide from the predators or because they have more resources). These species allocate less energy to early reproduction than their mainland relatives (reduced fecundity, longer development, longer lifespan, smaller little size, etc.).

Chapter 11

Conclusions

CONCLUSIONS

I. Predictive BM models are developed for the three groups of small mammals (rodents, lagomorphs and soricids), through statistical analysis, using data of teeth, cranial and postcranial bones of species of extant relatives. These models are statistically significant ($p < 0.05$, with some exception), with goodness-of-fit statistics and predictive errors that are more or less accurate and satisfactory depending on the phylogenetic group and the BM proxy used (measurement and postcranial element).

II. The following interpretations are drawn when the BM proxies are evaluated taking into consideration the accuracy (statistical values) and the subjective judgment (implementation to fossil register):

- Our analysis suggests that postcranial bones are better BM proxies than teeth. This results from the statistical discordant pattern of BM models and estimations between dental and postcranial elements, the essential function of postcranial bones as weight supports, and the absence of a direct functional principle that relates dental variables and BS increase. On the other hand, the only cranial variable introduced in the analysis gave satisfactory statistical result but it could not be tested in fossil remains.

- In general, stylopods (femora and humeri) provided more accurate models and, thus, we stand out that they are better proxies for BM estimation than zeugopods, which are highly modified for locomotion and habitat preference. In rodents and soricids, transversal or antero-posterior diameters of stylopods are the most satisfactory models, ruling out the lengths of long bones as suitable BM predictors. On the other hand, results from lagomorphs do not show this trend and the measurements of zeugopods and the length of long bones provided accurate estimations.

- In the case of soricids, we assessed the upper and lower dentition (molars) obtaining values of equal reliability in estimating the BM. However, the widths of upper and lower molars got poor statistical parameters and provided more heterogeneous BM predictions. Thus, we considered this measurement as an unreliable and unsuitable BM proxy.

- The most homogeneous models, obtained from splitting the database by either phylogeny (suborder or family) or locomotion, provided overall better statistical results than those models that comprise the whole database. In case of the few exceptions, the overrepresentation of one group with respect to another was considered one of the main causes of non-significant differences among allometric regression models of different groups.

- Statistically, multiple models are more satisfactory than bivariate ones. However, the former are of lower utilization in the case of small mammals as a consequence of the disconnection and fragmentation of bones during the sampling and screen-washing of remains.

III. The BMs of several fossil species of small mammals, including insular species and their mainland ancestor or relatives (when possible), were estimated using the allometric models developed previously. The BM values achieved contrast with previous estimations performed by other authors mostly because in our predictions: 1) teeth were not used as BM proxies (as long as postcranial elements were available) as these elements are highly modified in number and complexity in insular species, and 2) in the cases where teeth were used as proxy, the allometric models applied take in consideration the dental formulae of extant and extinct species. Therefore, the BM values obtained from our analyses are more accurate and reliable.

IV. The comparisons between the assessed BMs of fossil insular species and those of their mainland ancestors or extinct and extant relatives allow us to make the following considerations:

- Due to the absence of data of the ancestors and extinct relatives of the assessed rodents (*Canariomys bravoi* from Tenerife; *C. tamarani* from Gran Canaria; *Hypnomys onicensis* and *H. morpheus* from Mallorca; *Mikrotia magna* from Gargano; *Muscardinus cyclopeus* from Menorca) and leporids (*Nuralagus rex* from Menorca), the comparison with extant mainland species allow us to observe that the extinct species had larger BMs and we can consider them genuine insular giants.

- The BM comparison between extinct insular pikas (*Prolagus apricenicus* from Gargano; *P. figaro* and *P. sardus* from Sardinia) and their extinct and extant mainland relatives (*P.* cf. *calpensis*), allow us to observe that the former are larger (with the exception of *P. apricenicus* from older fissures) than the latter. In this case, we can also consider them as genuine insular giants.

- Finally, the BM comparisons between the insular extinct soricids (*Asoriculus burgioi* and *Crocidura sicula* subsp. from Sicily; *A. similis* from Sardinia; *C. zimmermanni* from Crete; anagenetic *Nesiotites* genera from Gymnesic Islands) with their ancestors (*A. gibberodon*, *C. kornfeldi*) and extinct and extant mainland relatives allow us to detect two trends: 1) *Asoriculus* and *Nesiotites* species had larger BM's than their extinct and extant relatives, hence, BM shifted towards gigantism; and 2) the extinct insular species of *Crocidura* are within the BM range of their ancestor and congeneric extant and extinct relatives, hence, their BMs remained unchanged.

V. The analyses performed in extinct small mammals provide evidence that the absence of predation is the primary driver in BS evolution under insular regimes. The number of predators is increased in larger and less isolated islands, entailing an absence of the gigantism expression. Our analyses also reveal that in absence of predation, resource availability can check the increase in BS. These paleontological results are in accordance with theoretical models and empirical evidences from extant species.

VI. The unexpected evolutionary BS increases (no fluctuations) of the assessed extinct insular species (populations or taxa forming an anagentic lineage) have been interpreted as a consequence of biotic factors (Red Queen Hypothesis), specifically of the high intraspecific competition of the density-dependent insular ecosystems. Thus, we consider that the isolation time (evolutionary time) is an important factor to taken into account in the studies of insular BS evolution.

VII. The study of femoral histology of Gargano's pikas revealed a longer life expectancy of this species than predicted from their BM. We consider that this species and, more generally, all small insular giant mammals move towards a slower life history (implying a longer lifespan and a delayed reproduction) as a result of the lower levels of extrinsic mortality seen in insular selective regimes. This provides empirical evidences for the theoretical model proposed by Palkovacs (2003) and is in accordance with previous genetic and morphological studies performed in current species of insular giants.

Chapter 12

References

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Chapter 13

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Alexis Castle (Always, Castle)

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