



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

## Bone histology of the giant fossil dormouse *Hypnomys onicensis* (Gliridae, Rodentia) from Balearic Islands



### *Histologie osseuse du loir géant fossile Hypnomys onicensis (Gliridae, Rodentia) des îles Baléares*

Guillem Orlandi-Oliveras<sup>a</sup>, Xavier Jordana<sup>a</sup>, Blanca Moncunill-Solé<sup>a</sup>,  
Meike Köhler<sup>a,b,\*</sup>

<sup>a</sup> Institut Català de Paleontologia Miquel Crusafont (ICP), ICTA-ICP, Edifici Z, c/de les Columnes, s/n., Campus de la UAB, 08193 Bellaterra, Barcelona, Spain

<sup>b</sup> ICREA at Institut Català de Paleontologia Miquel Crusafont (ICP), ICTA-ICP, Edifici Z, c/de les Columnes, s/n., Campus de la UAB, 08193 Bellaterra, Barcelona, Spain

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#### ABSTRACT

Insular gigantism is frequent in fossil and extant micromammals. It is widely assumed to result from increased food availability through expanded dietary niches under decreased interspecific competition. We compared the bone histology of the fossil giant dormouse *Hypnomys onicensis* (Gliridae) from the Balearic Islands with that of its closest living relative, *Eliomys quercinus*. Both display the same bone tissue types at similar ontogenetic stages, indicating comparable growth rates. Skeletochronological analysis shows that *Hypnomys* had an exceptionally long lifespan. Gigantism in insular *Hypnomys* hence results from a shift in life history toward the slow end of the slow–fast continuum.

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#### R É S U M É

Le gigantisme insulaire est fréquent chez les micro-mammifères vivants et fossiles. Il est largement admis que ceci résulte de la disponibilité accrue de nourriture, due à l'augmentation de niches alimentaires, en raison de la diminution de la compétition interspécifique. Le présent article compare l'histologie osseuse du loir géant fossile *Hypnomys onicensis* (Gliridae) des îles Baléares avec celle de son équivalent vivant le plus proche, *Eliomys quercinus*. Ces deux loirs présentent les mêmes types de tissu osseux à des stades ontogéniques similaires, indiquant des taux de croissance comparables. L'analyse squeletochronologique montre que *Hypnomys* a une durée de vie exceptionnellement longue. En conséquence, le gigantisme chez l'espèce insulaire *Hypnomys* résulte d'un glissement, dans l'histoire de la vie, vers le pôle lent d'un continuum lent–rapide.

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\* Corresponding author at: Institut Català de Paleontologia Miquel Crusafont (ICP), Edifici ICTA-ICP, c/de les columns s/n, Campus de la Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain.

E-mail address: meike.kohler@icp.cat (M. Köhler).

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## 1. Introduction

Dormice (Gliridae) are members of a peculiar rodent family characterized by a series of unusual traits. They exhibit torpor strategies with marked physiological cycles (Bieber and Ruf, 2009; Wilz and Heldmaier, 2000), an important plasticity in litter size and interbirth interval in adaptation to current resource availability (Pilastro et al., 2003), a strong trade-off between reproduction and future survival (Ruf et al., 2006), and a slow life history with a long life span in relation to their body size (Moreno, 2002). These highly plastic traits make dormice especially suitable for life under precarious resource conditions, a critical characteristic to survival during long drifts on wood over sea and colonization of islands. Thus, dormice represent a large part of giant endemisms on certain Mediterranean islands, for instance *Hypnomys* Bate, 1918 on Mallorca, *Muscardinus cyclopeus* Agustí et al., 1982 on Menorca (Moncunill-Solé et al., 2014), and the even larger taxa *Leithia* Lydekker, 1896 and *Maltamys* Zammit Maempel and de Bruijn, 1982 on Sicily and Malta (Nadachowski and Daoud, 1994).

*Hypnomys* is an extinct giant genus from the Gymnesian Islands (Majorca and Minorca, Spain) that appeared after a single Messinian colonization event on Mallorca, and then colonized Menorca probably during the first Late Pliocene glaciations. *Hypnomys morpheus* Bate, 1919 is the most recent representative of a clade that evolved in isolation during the last 5.35 million years until Late Holocene (Alcover et al., 1981). *Hypnomys onicensis* Reumer, 1994, however, was an early species of that anagenetic lineage with an estimated body mass of approximately 200 g (Moncunill-Solé et al., 2014), being almost two and a half times heavier than its closest mainland relative, the extant garden dormouse *Eliomys* Linnaeus, 1766 (Bover et al., 2008; McKenna and Bell, 1997) which weighs 82.5 g (Tacutu et al., 2013). Besides the larger body mass, *Hypnomys* differs from *Eliomys* in shape and dimensions of cranial and postcranial elements, suggesting differences in locomotion, foraging, and food processing (Bover et al., 2010; Quintana and Moncunill-Solé, 2014). The extraordinary preservation of the *Hypnomys* fossil material offers the opportunity to study some life history traits such as maturity, longevity and growth rate in order to improve our understanding of the evolution of gigantism on islands.

Insular gigantism is widely assumed to result from growth rate acceleration in response to increased food levels (McNab, 1994, 2010, 2012; Pafilis et al., 2009 and references therein). Though islands are generally considered to be resource-poor for large mammals (McNab, 2012), the decreased number of species in insular ecosystems is considered to allow small mammals to expand their dietary niche (van der Geer, 2005) and, hence, the quantity of available resources (McNab, 2010 and references therein).

To test whether insular gigantism results from accelerated growth (and, by implication, a shift towards a fast life history), or whether it instead results from a prolonged growth period (and, by implication, a shift towards a slow life history), we studied bone tissues and the number of growth marks (skeletochronology) of ontogenetic series of the insular giant dormouse *H. onicensis* and the continental sister taxon *Eliomys quercinus*.

## 2. Material and methods

The study is based on the analysis of bone tissue patterns and growth marks observed in mid-shaft femoral sections with polarized light microscopy.

The material analyzed consists of a total of 48 femora, 40 belonging to *H. onicensis* and 8 to the extant taxon *E. quercinus*. The *H. onicensis* femora come from the fossil site “Sa Pedrera de S’Ònix” on Mallorca island, which dates from the Late Pliocene. The femora of the extant taxa sample were also analyzed and discussed in García-Martínez et al. (2011). One of these, labeled therein as “ID 15”, had been misidentified as *Glis glis* Linnaeus, 1766. The data sample is displayed in supplementary material, Table S1, providing information on locality, stratigraphic age, anteroposterior diaphyseal diameter (mm), number of Lines of Arrested Growth and other observations. Epiphyseal fusion is not taken into account, as many of the *H. onicensis* femora are represented only by proximal or distal thirds. Furthermore, the epiphyseal fusion of the *H. onicensis* shows no correlation with age, because epiphyses remain unfused even in very old individuals.

The fossil material belongs to the collections of the Institut Català de Paleontologia Miquel Crusafont (ICP) (Spain), whereas the extant material comes from the collections of the Museu de Ciències Naturals de Granollers. For more information see García-Martínez et al. (2011). The thin sections of both species are stored at ICP with the acronym IPS.

Once the material was prepared and ready for sectioning, the femora were embedded in epoxy resin and slides were prepared following the protocol described in García-Martínez et al. (2011). The obtained slides were observed under circularly polarized transmitted light (Leica DM 2500 P). We considered growth marks as LAGs when they can be traced around the periphery of the bone (Horner et al., 1999). The descriptions of bone tissues are based on the typological classification established by de Ricqlès et al. (1991) and de Margerie et al. (2002). We counted double LAGs, frequent in both taxa, as representing only one year.

### Abbreviations:

**EFS:** External Fundamental System.

**FLC:** Fibro-Lamellar Complex.

**IFS:** Internal Fundamental System.

**LAG:** Line of Arrested Growth.

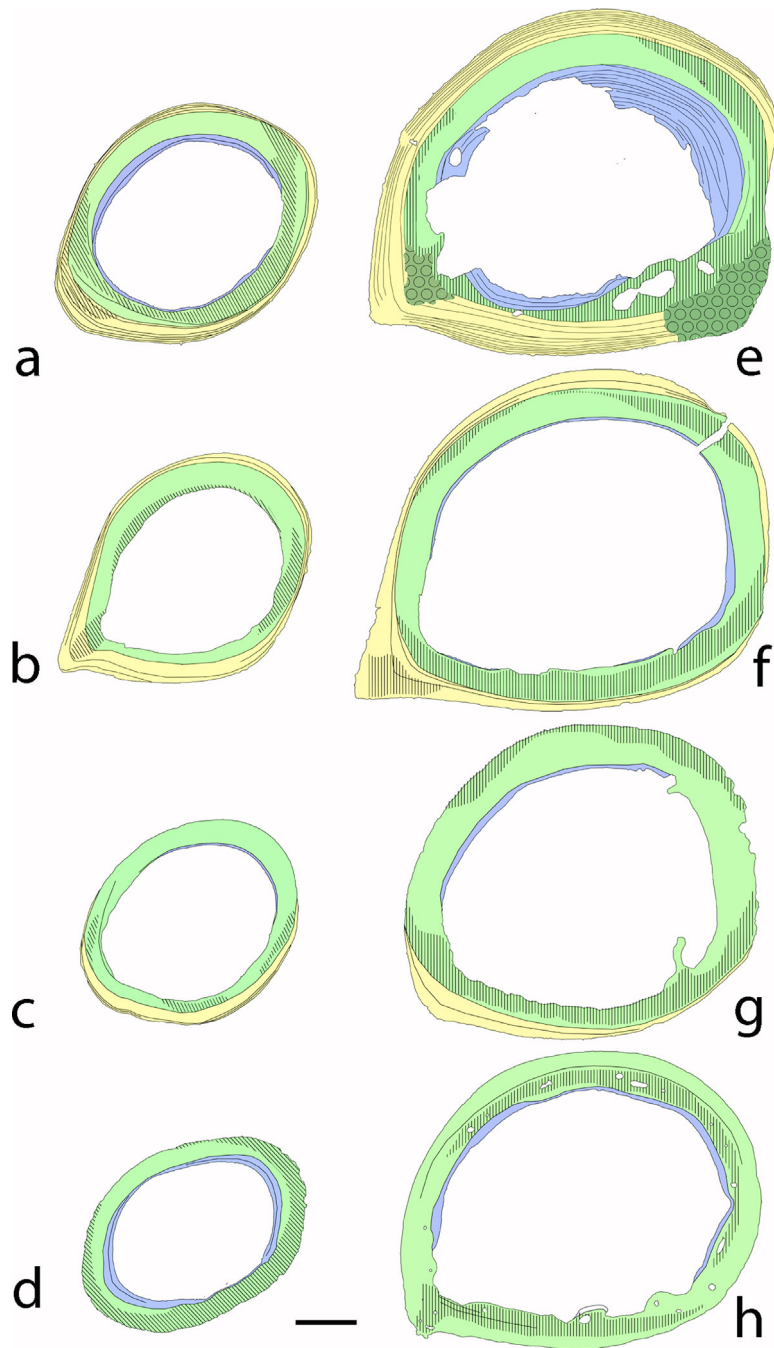
**LNV:** Lamellar (or parallel-fibered) Non-Vascular.

**LPO:** Lamellar (or parallel-fibered) with Primary Osteons.

**LSV:** Lamellar (or parallel-fibered) Simple Vascular.

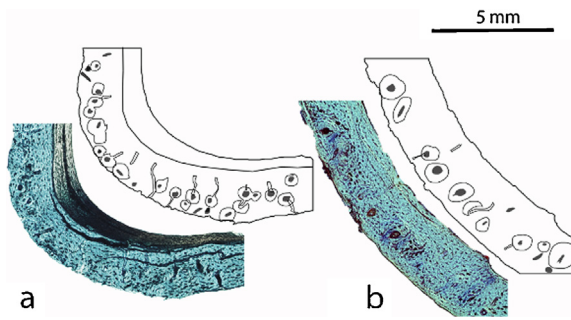
## 3. Results

Of the *H. onicensis* sample, 32 slides were sufficiently well preserved for visualization of the tissue pattern and to observe the presence of growth marks. Of these femora, only five pertained to young individuals that had not yet attained reproductive maturity, as they did not develop an EFS. On the other hand, the great majority are adult individuals presenting two or three LAGs in the EFS corresponding to an age of two–three years. We also found older exemplars, with nine individuals providing an estimated



**Fig. 1.** (Color online.) Ontogenetic series of femora of *Eliomys quercinus* (left) and *Hypnomys onicensis* (right). Green areas provide the outline of the juvenile/adult transition. Dashed areas: limited regions with primary osteons, either lamellar (or parallel-fibered) with primary osteons (LPO) or fibro-lamellar complex (FLC). Yellow areas: incremental growth after maturity (EFS). Blue areas around the medullary cavity: internal fundamental systems (IFS). Specimen's collection numbers and age for *E. quercinus* top down: a: IPS 82128a, oldest individual, 6 line of arrested growths (LAGs); b: IPS 82130a, 2 LAGs; c: IPS 82129b, 1 LAG; d: IPS 82133, 0 LAGs. Specimens' collection numbers and age for *H. onicensis* top down: e: IPS 83489, one of the oldest individual, > 10 LAGs; f: IPS 82106, 2 LAGs; g: IPS 82095, 2 LAGs; h: IPS 82092, 0 LAGs. Scale bar 5 mm.

**Fig. 1.** (Couleur en ligne.) Série ontogénique des fémurs d'*Eliomys quercinus* (gauche) et d'*Hypnomys onicensis* (droite). Les zones colorées en vert indiquent le contour de la transition juvénile/adulte. Zones hachurées : régions limitées contenant des ostéones primaires, qu'elles soient lamellaires (ou à fibres parallèles), avec des ostéones primaires ou un complexe fibro-mamellaire. Zones jaunes : croissance incrémentale après maturation (EFS). Zones bleues autour des cavités médullaires : systèmes fondamentaux internes (IFS). Références des spécimens en collection et âge pour *E. quercinus* (de haut en bas) : a : IPS 82128a, le plus vieil individu, six lignes de croissance arrêtée (LAGs) ; b : IPS 82130a, 2 LAGs ; c : IPS 82129b, 1 LAG ; d : IPS 82133, 0 LAGs. Numéros des spécimens en collection et âge pour *H. onicensis* (de haut en bas) : e : IPS 83489, un des plus vieux individus, > 10 LAGs ; f : IPS 82106, 2 LAGs ; g : IPS 82095, 2 LAGs ; h : IPS 82092, 0 LAGs. Échelle : 5 mm.



**Fig. 2.** (Color online.) Areas with primary osteons that correspond to dashed areas on Fig. 1. Left: juvenile *Eliomys quercinus*: a: IPS 82133; right: juvenile *Hypnomys onicensis*: b: IPS 82081. Observe the smaller but more abundant primary osteons in *E. quercinus*.

**Fig. 2.** (Couleur en ligne.) Zones comprenant des ostéons primaires qui correspondent aux zones hachurées sur la Fig. 1. Gauche : *Eliomys quercinus* juvénile : a : IPS 82133 ; droite : *Hypnomys onicensis* juvénile : b : IPS 82081. NB : les ostéons primaires sont plus petits, mais plus abondantes chez *E. quercinus*.

age of at least five years. From these older individuals, two exhibit more than eight, and two more than 10 LAGs in the EFS. The eight slides of the extant continental taxon (*E. quercinus*) included three immature individuals; the rest belongs to specimens with lines of arrested growth in their EFS. Only two femora exhibit more than four LAGs. Skeletochronological results for the whole sample are shown in [supplementary material, Table S1](#).

Juveniles of both *H. onicensis* and *E. quercinus* exhibit relatively fast-growing tissues. In both taxa, the medullary cavity is relatively expanded, so that the preserved cortex most likely represents postnatal growth only. The tissue consists of scarcely-vascularized or avascular parallel-fibered matrix (LSV-LNV) and of limited regions of woven bone (fibro-lamellar complex [FLC]). Tissue with primary osteons (LPO, FLC) extends predominantly from the internal part of the posterior region (insertion area of the third trochanter at a later stage) along the posterior cortex, and over a small and isolated area at the right lateral part of the anterior region (Fig. 1 d and h). Frequently, a resorption (cement) line delimits these areas that follow the curved margins of the primary osteons. This line is not the first LAG, though both structures may coincide. After deposition of the resorption line, growth rate slows down (parallel-fibered matrix, mainly LSV) until deposition of the first LAG. Vascularization, where present, is mostly longitudinal; some radial vessels, however uncommon, are found in both taxa. An inner cortical layer, if present, is thin and unevenly distributed, and is generally located in the anterior region. It may be deposited at a very early juvenile stage (Fig. 1), but usually it appears at a late juvenile or early adult stage.

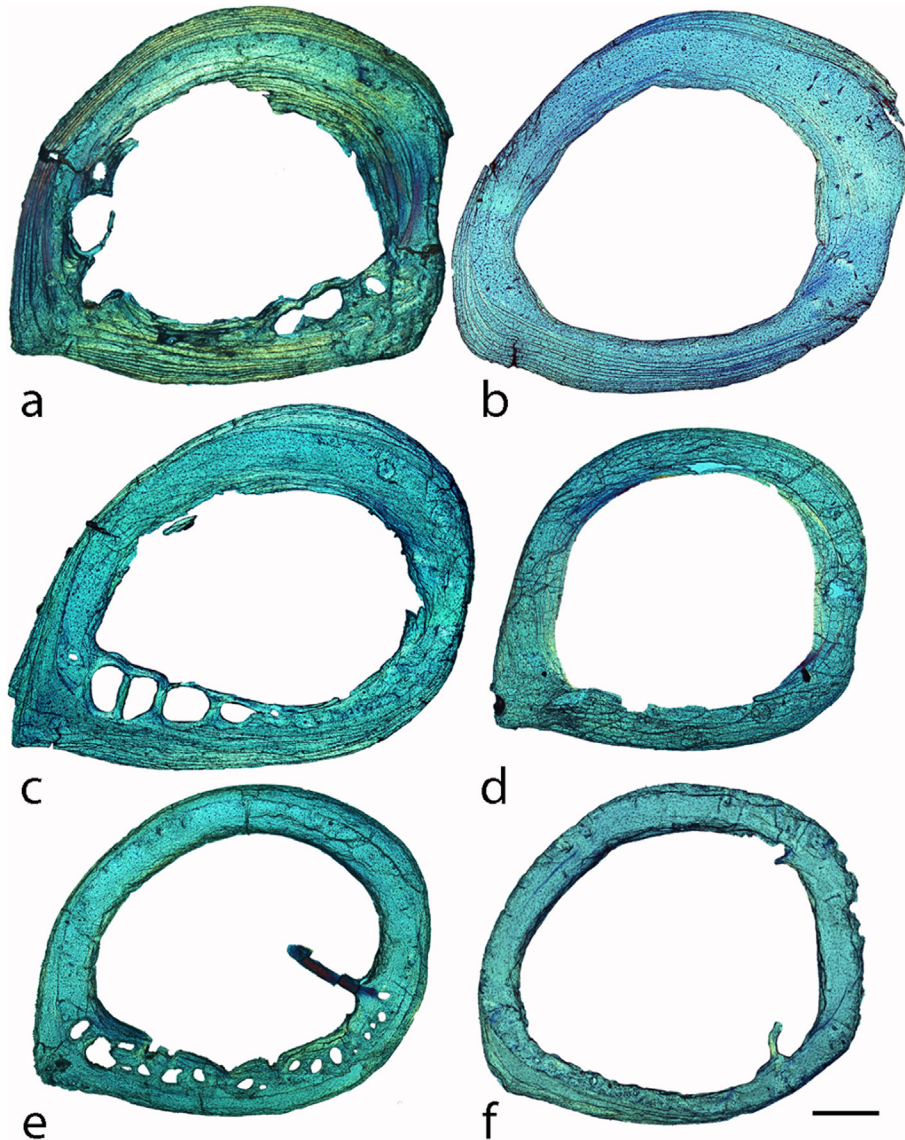
*H. onicensis* differs from *E. quercinus* in some aspects. The juvenile cortical wall is slightly broader than in *E. quercinus* as expected from allometry for a larger species. Primary osteons in the FLC of *H. onicensis* are slightly larger in diameter (Fig. 2). Unlike *E. quercinus*, several juveniles of *H. onicensis* show large resorption cavities in their FLC or LPO matrix in the place of former primary osteons (Fig. 3).

Adults of both taxa show at least one LAG. The almost entirely avascular lamellar cortex (LNV) of adults indicates a similarly slow growth rate for *H. onicensis* and *E. quercinus*. The area of the third trochanter begins to form at the medial-posterior edge approximately during the second year of life; usually, apposition in this area is accelerated over a short time (LPO-FLC). In some individuals, LAGs are irregularly spaced; however, regular apposition of double LAGs is not uncommon (Fig. 4). In both taxa, Haversian systems perforated the FLC and LPO cortex of older individuals (Fig. 1e). Contrary to *E. quercinus*, old *H. onicensis* individuals are frequent in our sample ([supplementary material, Table S1](#)) and they can double the age of old *E. quercinus* individuals. Related to extended longevity, old *Hypnomys* specimens show a very extensive and broad inner cortical layer (Fig. 1) and a higher degree of remodeling. While most “middle-aged” *H. onicensis* do not show any sign of resorption within their cortex but only the typical and steadily progressing resorption front at the medullary margin, young adults and very old individuals frequently show large resorption areas within the primary FLC (Fig. 3). This pattern is not found in *E. quercinus*.

#### 4. Discussion

There is a general agreement on the causes that trigger insular gigantism. The widely accepted hypothesis is that under decreased interspecific competition (low species diversity on islands results from low resource levels, McNab, 1994, 2012), small mammals expand their dietary niche. The thus increased resource supply permits an accelerated growth leading to a larger body size, which is possible under absence of predation and favoured by natural selection under increased intraspecific competition (see McNab, 2010 and literature therein). Bone and dental histology are the most suitable tools to reconstruct life history traits in fossil vertebrates. Using bone histology, we test the hypothesis that insular gigantism results from an increase in growth rate triggered by increased resource abundance.

Several features suggest that the giant insular dormouse *H. onicensis* from Balearic Islands did not grow at the same rate but over a longer time period than its closest continental relative *E. quercinus*. Both species deposit the same tissue types at comparable ontogenetic stages. The earliest ontogenetic stage, the age until weaning, was not available, most likely because at that age juveniles do not leave their nests. After weaning, juveniles lay down a matrix of avascular or poorly vascularised parallel-fibered bone with simple vascular canals and, in small regionally limited spots, parallel-fibered bone with primary osteons or even woven bone. Late juveniles deposit poorly vascularised or avascular lamellar bone, and adults form an EFS of avascular lamellar bone with LAGs. Because bone tissue types record the rate of bone apposition (Amprino, 1947; de Margerie et al., 2002), the similarities in bone histology between the giant insular dormouse and its small continental relative strongly suggest that they grew at similar rates. The functional implication of slight differences in the diameter and density of primary osteons between both species, however, are controversial. Both osteonal size and density have previously been used to calculate bone growth



**Fig. 3.** (Color online.) Sequence of ontogenetic stages in *Hyponymys onicensis* exhibiting strong resorption of the lamellar (or parallel-fibered) with primary osteons (LPO)/fibro-lamellar complex (FLC) regions (left) and individuals without resorption (right): a: IPS 83489 - > 10 line of arrested growths (LAGs); b: IPS 82084 - 8 LAGs; c: IPS 82091 - 4 LAGs; d: IPS 82089 - 3 LAGs; e: IPS 82108 - 1 LAG; f: IPS 82095 - 2 LAGs. Scale bar: 5 mm.

**Fig. 3.** (Couleur en ligne.) Séquence des stades ontogéniques chez *Hyponymys onicensis* montrant une forte résorption des régions lamellaires (ou à fibres parallèles), à ostéones primaires (LPO), ou complexe fibro-lamellaire (FLC) (gauche) et certains individus sans résorption (droite) : a : IPS 83489 - > 10 lignes de croissance arrêtée (LAGs) ; b : IPS 82084 - 8 LAGs ; c : IPS 82091 - 4 LAGs ; d : IPS 82089 - 3 LAGs ; e : IPS 82108 - 1 LAG ; f : IPS 82095 - 2 LAGs. Échelle : 5 mm.

rate (de Margerie et al., 2002). The authors concluded that the bigger the cavities of primary osteons, the faster the growth rate, whereby they observed: “the osteon diameter is an indirect estimation of the osteonal fraction of the tissue, bigger osteons being closer to each other” (p. 226). Thus, both size and density of primary osteons reflect tissue growth rate (de Margerie et al., 2002). In the case of *H. onicensis* and *E. quercinus*, primary osteons in regionally limited cortical spots are slightly larger in the giant dormouse (Fig. 2). However, the primary osteons are less abundant and similar or even less closely packed at

comparable age; the osteonal fraction, hence, is equal or smaller in the larger species (Fig. 2). This means that while the somewhat larger size of the primary osteons suggests a slightly faster growth rate, the osteonal density indicates a slightly slower growth rate. Considering that the study of de Margerie et al. (2002), based on an ontogenetic series of one sole species (*Anas platyrhynchos*), did not take into account interspecific allometry, we suggest that this feature might result from a scaling effect rather than from differences in growth rate. An allometric analysis on primary osteon size is needed.



**Fig. 4.** Close-up of IPS 82084 with regularly deposited double line of arrested growths.

**Fig. 4.** Zoom sur IPS 82084 avec des doubles lignes de croissance arrêtée régulièrement déposées.

Not only adults but also early juveniles of *Hypnomys* (tentatively aged as “postweaning before the first winter” because of their close-to-adult size and the lack of LAGs, Fig. 1d and h) are much larger than *Eliomys* of comparable age (see supplementary material, Table S1 for sample size). The size differences between both species at the earliest available ontogenetic stage, raises the question of whether a faster growth rate or a prolonged growth period (or both) accounts for the larger size of juvenile *Hypnomys*. As discussed above, both taxa deposit the same tissue type from the earliest preserved juvenile stage (innermost cortical wall of youngest individuals) until old adults. This excludes differences in growth rate for almost the entire growth period. Though we cannot rule out that a faster intrauterine growth rate accounts for a larger size of *Hypnomys* after birth, the supposition of a longer gestation period seems more appropriate given the allometric scaling relationship between gestation time and body size (Lindstedt and Calder, 1981).

A similar line of reasoning applies to the differences in thickness of the cortical wall between both species. Because the cortical wall of terrestrial vertebrates has to withstand strains and stresses generated by weight bearing, locomotion, and other activities, variance in thickness can result from differences in life style or may simply reflect body size allometry. Some authors suggested a fossorial life style for *Hypnomys* (Bover et al., 2010, but see Quintana and Moncunill-Solé, 2014 for a different interpretation). Nevertheless, the differences in thickness between the cortical walls of *Hypnomys* and *Eliomys* are only modest at comparable ages, which are most parsimoniously accounted for by simple body size allometry. Accordingly, the slightly larger juvenile cortical area in *H. onicencis* suggests a somewhat longer growth period (at a similar growth rate) until attainment of maturity as expected from the correlation between body size and age at maturity (Lindstedt and Calder, 1981).

The many LAGs found in the EFS of the oldest *H. onicencis* individuals that double those of *E. quercinus* incontrovertibly document an important increase in longevity. The attainment of fairly old ages in *H. onicencis* led to an increased incidence of osteoporotic resorption cavities in the cortical area of older individuals, especially in those older than 10 years (Fig. 3a). The relatively high frequency of large resorption cavities at very young ages might instead indicate nutritional problems, an explanation congruent with the notion of resource limitation as a principle characteristic of insular environments (McNab, 1994; Palkovacs, 2003).

Life history traits correlate with body size, and one might argue that an increase in body mass must be associated with an increase in age at maturity and longevity. Testing whether the observed increase in longevity is predicted from allometry is problematic, because extant dormice taxa are all small, which makes it impossible to plot a regression line based on dormice that extends up to giant *Hypnomys*. Including in that plot other rodents such as murids does not make sense, since dormice have an exceptionally slow life history for their body mass, requiring comparison within the taxon Gliridae. However, the important increase in longevity from 5.5 years in 82 g *Eliomys* (Tacutu et al., 2013) to more than 10 years in closely related 200 g *H. onicencis* contrasts with the unchanged longevity (max. four years) between 20 g *Mus musculus* and 200 g *Rattus rattus*, (Tacutu et al., 2013). This strongly suggests that the doubling of longevity from *E. quercinus* to *H. onicencis* exceeds by far what is expected from size scaling. Thus, taking together the similarity in growth rate and the important increase in longevity, we conclude that gigantism in *Hypnomys* does not result from accelerated growth but from a deceleration of the pace of the life cycle, that is a delay in key life history features (age at maturity and longevity).

Finally, the frequent appearance of evenly spaced double LAGs in many individuals is intriguing (Fig. 4) and only exceptionally observed in other small mammals such as murids (personal observation MK). We speculate that this pattern is related to dormancy in dormice, reflecting two periods of dormancy, cold winter and hot dry summer. More research, particularly experiments with fluorescent markers, is needed to understand the formation of double-spaced LAGs in dormice.

## 5. Conclusions

Our histological study on long bone tissues of the giant insular dormouse *H. onicencis* in comparison with that of the continental closest relative *E. quercinus* provides evidence of an unchanged (in relation to the closest mainland relative) postnatal growth rate. This was likely associated with changes in time rather than in rate of foetal growth during gestation, leading to a larger size in early juveniles. Increased cortical thickness, in combination with a similar growth rate, suggests that *Hypnomys* attained sexual maturity somewhat later than *Eliomys*. Skeletochronology provides evidence of an extended maximum life span of more than 10 years, doubling the age of the oldest *Eliomys* individuals. These results do not lend support to the widely accepted hypothesis that insular giants evolved through

faster growth rates in an environment with abundant resources.

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### Appendix A. Supplementary material

Supplementary material associated with this article can be found in the online version available at <http://dx.doi.org/10.1016/j.crpv.2015.05.001>.

### References

- Alcover, J.A., Moyà-Solà, S., Pons-Moyà, J., 1981. Les quimeres del pasat: els vertebrats fòssils del Plio-Quaternari de les Balears i Pitiüses. Editorial Moll, Ciutat de Mallorca, Mallorca (265 p.).
- Amprino, R., 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. *Arch. Biol.* 58, 315–330.
- Bate, D.M.A., 1918. On a new genus of extinct Muscardine Rodent from the Balearic Islands. *Proc. Zool. Soc. London* 88, 209–222.
- Bieber, C., Ruf, T., 2009. Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturw.* 96, 165–171.
- Bover, P., Quintana, J., Alcover, J.A., 2008. Three islands, three worlds: paleogeography and evolution of the vertebrate fauna from the Balearic Islands. *Quatern. Int.* 182, 135–144.
- Bover, P., Alcover, J.A., Michaux, J.J., Hautier, L., Hutterer, R., 2010. Body shape and life style of the extinct Balearic Dormouse *Hypnomys* (Rodentia, Gliridae): new evidence from the study of associated skeletons. *PLoS One* 5, e15817.
- de Margerie, E., Cubo, J., Castanet, J., 2002. Bone typology and growth rate: testing and quantifying “Amprino’s rule” in the mallard (*Anas platyrhynchos*). *C. R. Biologies* 325, 221–230.
- de Ricqlès, A., Meunier, F.J., Castanet, J., Francillon-Vieillot, H., 1991. Bone matrix and bone specific products. In: Hall, B.K. (Ed.), *Bone*, vol. 3. CRC Press, Boca Raton, London, pp. 85–124.
- García-Martínez, R., Marín-Moratalla, N., Jordana, X., Köhler, M., 2011. The ontogeny of bone growth in two species of dormice: reconstructing life history traits. *C. R. Palevol* 10, 489–498.
- Horner, J., de Ricqlès, A., Padian, K., 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* 25, 295–304.
- Lindstedt, S.L., Calder III, W.A., 1981. Body size, physiological time, and longevity of homeothermic animals. *Quart. Rev. Biol.* 56 (1), 1–16.
- McKenna, M.C., Bell, S.K., 1997. *Classification of Mammals Above the Species Level*. Columbia University Press, New York (631 p.).
- McNab, B.K., 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. *Am. Nat.* 144 (4), 643–660.
- McNab, B.K., 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia* 164, 13–23.
- McNab, B.K., 2012. *Extreme Measures: The Ecological Energetics of Birds and Mammals*. University of Chicago Press, Chicago (322 p.).
- Moreno, S., 2002. Lirón caretto *Eliomys quercinus* (Linnaeus, 1766). *Galemys* 14, 1–16.
- Moncunill-Solé, B., Jordana, X., Marín-Moratalla, N., Moyà-Solà, S., Köhler, M., 2014. How large are the extinct giant insular rodents? New body mass estimations from teeth and bones. *Integr. Zool.* 9, 197–212.
- Nadachoswki, A., Daoud, A., 1994. Patterns of Myoxid evolution in the Pliocene and Pleistocene of Europe. *Hystrix* (n.s.) 6, 141–149.
- Pafilis, P., Meiri, S., Foufopoulos, J., Valakos, E., 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften*. 96 (9), 1107–1113, <http://dx.doi.org/10.1007/s00114-009-0564-3>.
- Palkovacs, E.P., 2003. Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* 103, 37–44.
- Pilastro, A., Tavecchia, G., Marín, G., 2003. Long living and reproduction skipping in the fat dormouse. *Ecology* 84, 1784–1792.
- Quintana, J., Moncunill-Solé, B., 2014. Reconsidering locomotor habits and life style of the Balearic insular giant rodent *Hypnomys* Bate, 1918 from the allometry of the limb long bones. *C. R. Palevol* 13, 297–306.
- Ruf, T., Fietz, J., Schlund, W., Bieber, C., 2006. High survival in poor years: life history tactics adapted to mast seeding in the edible dormouse. *Ecology* 87, 372–381.
- Tacutu, R., Craig, T., Budovsky, A., Wuttke, D., Lehmann, G., Taranukha, D., Costa, J., Fraifeld, V.E., de Magalhães, J.P., 2013. Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Res.* 41 (D1), D1027–D1033.
- van der Geer, A.E., 2005. Island ruminants and parallel evolution of functional structures. *Quat.* 2, 231–240.
- Wilz, M., Heldmaier, G., 2000. Comparison of hibernation, estivation and daily torpor in the edible dormouse, *Glis glis*. *J. Comp. Physiol. B* 170, 511–521.