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Reconsidering locomotor habits and life style of the Balearic insular giant rodent *Hypnomys* Bate, 1918 from the allometry of the limb long bones

Nouveau regard sur les modes de locomotion et le style de vie du rongeur insulaire géant des Baléares, Hypnomys *Bate, 1918 à partir de l'examen des os longs de membres*

Josep Quintana Cardona [a,b,*], Blanca Moncunill-Solé [a]

[a] *Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain*
[b] *C/Gustau Mas 79-1er, 07760 Ciutadella de Menorca, Illes Balears, Spain*

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ABSTRACT

The genus *Hypnomys* Bate, 1918 includes some endemic Neogene chronospecies from Mallorca and Menorca, evolved in insularity conditions from the Lower Pliocene to the human arrival at the archipelago. The study of the allometric proportions (functional length and sagittal diameter) of the limbs' long bones of *Hypnomys eliomyoides* Agusti, 1980 (Lower Pleistocene of Menorca), *Hypnomys* sp. (Pleistocene of Menorca), *Hypnomys onicensis* (Reumer, 1994) (Upper Pliocene-Lower Pleistocene of Mallorca) and *Hypnomys morpheus* Bate, 1918 (Upper Pleistocene of Mallorca) only indicates small differences with the garden dormouse (*Eliomys quercinus* Linnaeus, 1776) and other mainland rodents and insectivores. The study about the locomotion type by means of Similarity Matrix of Bou indicates that 1) *Hypnomys* spp. presents the greater similarities with the arboreal, jumping and gliding species; 2) the jumping and digging life style of *Hypnomys* spp. are more developed (25%) than in *E. quercinus*; 3) the walking locomotion of *Hypnomys* spp. is only a 7% greater than in *E. quercinus*; and 4) the degree of similarity with the gliding locomotion of *Hypnomys* sp. is greater (17%) than in *E. quercinus*. Some of this data indicates that *Hypnomys* spp. was better adapted to the arboreal life than *E. quercinus*, due to the relationship between the jumping and gliding capacities with the arboreal locomotion. The greater similarity of *Hypnomys* spp. with the walking locomotion does not necessarily involve more terrestrial habits. Our interpretation contrasts with earlier conclusions of *Hypnomys* life style (*Hypnomys* cf. *onicensis* and *Hypnomys morpheus*) where the terrestrial locomotion was overestimated in front of the arboreal locomotion. The locomotion type of *Hypnomys* would be related with the presence of important forest masses on the Balearic Islands during the Neogene, a

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[*] Corresponding author.
E-mail addresses: picoguevo@hotmail.com, Pangea.aion@hotmail.com (J. Quintana Cardona), blanca.moncunill@icp.cat (B. Moncunill-Solé).

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different degree of environmental stress from that of the mainland ecosystems and a probable expansion of the ecological niche occupied by these species.

RÉSUMÉ

Mots clés :
Faunes insulaires néogènes
Méditerranée occidentale
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Tendances locomotrices
Niche écologique
Oiseaux de proie

Le genre *Hypnomys* Bate, 1918 inclut certaines chrono-espèces néogènes endémiques de Majorque et Minorque, qui ont évolué dans des conditions insulaires, depuis le Pliocène inférieur jusqu'à l'arrivée de l'Homme sur l'archipel. L'étude des proportions allométriques (longueur fonctionnelle et diamètre sagittal) des os longs d'*Hypnomys eliomyoides* Agusti, 1980 (Pléistocène inférieur de Minorque), *Hypnomys* sp. (Pléistocène de Minorque), *Hypnomys obicensis* (Reumer, 1994) (Pliocène supérieur–Pléistocène inférieur de Majorque) et *Hypnomys morpheus* Bate, 1918 (Pléistocène supérieur de Majorque) n'indique que de petites différences par rapport au loir de jardin (*Eliomys quercinus* Linnaeus 1776) et à d'autres rongeurs et insectivores terrestres. Une analyse du type de locomotion au moyen de la *Similarity Matrix* (matrice de similitude) de Bou indique : 1) que *Hypnomys* spp. présente les plus grandes ressemblances avec les espèces arboricoles, sauteuses et glisseuses ; 2) que les modes de vie de type saut et creusement d'*Hypnomys* spp. sont plus dérivés (25 %) que chez *E. quercinus* ; 3) que le mode locomoteur de marche d'*Hypnomys* spp. est seulement supérieur de 7 % à celui d'*E. quercinus* ; et 4) que le degré de ressemblance avec la locomotion de type glisse d'*Hypnomys* sp. est supérieur de 17 % chez *E. quercinus*. Certaines de ces données indiquent qu'*Hypnomys* spp. était mieux adapté à la vie arboricole qu'*E. quercinus*, d'après des ressemblances déduites de ses capacités de saut et de glisse et celles de la locomotion arboricole. La plus grande ressemblance d'*Hypnomys* spp. concernant des traits corrélatifs de la locomotion de type marche n'implique pas nécessairement de mode de vie plus terrestre. Notre interprétation contraste avec des conclusions antérieures sur le style de vie d'*Hypnomys* (*Hypnomys* cf. *onicensis* et *Hynomys morpheus*), selon lesquelles la locomotion terrestre a été surestimée en comparaison de la locomotion arboricole. Le mode de locomotion d'*Hypnomys* serait lié à la présence d'importantes zones forestières sur les Baléares pendant le Néogène, un degré de stress environnemental différent de celui des écosystèmes terrestres et une probable expansion des zones, nécessitant une adaptation pour ces espèces.

1. Introduction

The vertebrates evolved in insularity conditions show changes affecting size and body proportions, locomotion type, behavior, physiology, life cycle and ecological niche (Alcover, 1988a,b; Azzaroli, 1971; Köhler and Moyà-Solà, 2009; McNab, 2002; Sondaar, 1977; Van der Geer et al., 2010). These changes are well documented in endemic terrestrial mammals from the Miocene, Pliocene and Pleistocene of the Balearic Islands (Agusti et al., 1982; Alcover et al., 1981, 1999; Bate, 1909, 1918, 1944; Jordana et al., 2012; Köhler, 2010; Köhler and Moyà-Solà, 2001, 2004, 2009; Quintana, 1993; Quintana and Agustí, 2007; Quintana et al., 2011). Studies about locomotion and body proportions have been focused principally on large mammals (the fossil Balearic goat, *Myotragus balearicus* Bate, 1909 [Bover et al., 2005; Köhler and Moyà-Solà, 2001, 2004; Leinders, 1979; Leinders and Sondaar, 1974; Moyá-Solá, 1979; Sondaar, 1977] and the giant rabbit of Minorca, *Nuralagus rex* Quintana, et al., 2011, while those related with rodents and insectivores of small size, including the genus *Hypnomys* Bate, 1918 (Bover et al., 2010; García-Martínez et al., 2011; Mills, 1976; Quintana and Arnau, 2004), *Muscardinus* Kaup, 1829 (Gliridae), *Tragomys* Agusti, et al., 2012 (Cricetidae) and *Nesiotites* Bate, 1944 (Soricidae), have been scarce or inexistent.

A recent study of the body shape and life style of *Hypnomys* cf. *onicensis* (Reumer, 1994) and *Hypnomys morpheus* Bate, 1918 from Mallorca based on statistical analyses (factorial discriminant analysis and postcranial indexes), offers complex results that do not allow clear conclusions (Bover et al., 2010: p. 9). These authors affirm that these two species showed a more terrestrial and fossorial life style and proportionally more elongated zeugopodium than the extant garden dormouse (*Eliomys quercinus* Linnaeus, 1766).

2. Objectives

In view of the Bover et al. (2010) conclusions, we would like to compare their results using an alternative method (Similarity Matrix of Bou), in order to know with more precision the locomotion type and allometric changes in zeugopodium (tibia and ulna) and stylopodium (femur and humerus) of *Hypnomys* from five paleontological deposits from Menorca and Mallorca. Moreover, we think that it would be interesting to compare several island species with important body mass differences (*Hypnomys* spp. versus *M. balearicus* and *N. rex*), for knowing if limbs proportions have changed similarly in all cases, as both *M. balearicus* and *N. rex* show shorter limbs compared to mainland bovids and leporids respectively (Quintana et al., 2011; Sondaar, 1977).

Fig. 1. Location of the studied deposits with *Hypnomys* spp. 1: Barranc de Binigaus (*H. eliomyoides*); 2: Sa Cigonya (*Hypnomys* sp.1); 3: deposit 17 from Punta Esquitxador (*Hypnomys* sp.2); 4: Sa Pedrera de s'Ònix (*H. onicensis*); 5: Sa Cova de sa Bassa Blanca (*H. morpheus*).

Fig. 1. Localisation des dépôts à *Hypnomys* spp. étudiés. 1 : Barranc de Binigaus (*H. eliomyoides*) ; 2 : Sa Cigonya (*Hypnomys* sp.1) ; 3 : dépôt 17 de Punta Esquitxador (*Hypnomys* sp.2) ; 4 : Sa Pedrera de s'Ònix (*H. onicensis*) ; 5 : Sa Cova de sa Bassa Blanca (*H. morpheus*).

3. Methods

3.1. Samples

Studied samples come from three sites in Menorca (Barranc de Binigaus: *Hypnomys eliomyoides* Agusti, 1980 [Lower Pleistocene]; Sa Cigonya: *Hypnomys* sp.1 [Pleistocene]; deposit 17 from Punta Esquitxador: *Hypnomys* sp.2 [Pleistocene]) and from two sites in Mallorca (Pedrera de s'Ònix: *Hypnomys onicensis* [Upper Pliocene–Lower Pleistocene]; Cova de sa Bassa Blanca: *H. morpheus* [Upper Pleistocene]) (Fig. 1). The complete descriptions of these deposits are in Moyà-Solà and Pons-Moyà (1979, 1980) (Cova de sa Bassa Blanca and Barranc de Binigaus), Alcover et al. (1981) (Pedrera de s'Ònix) and Quintana (1998) (Sa Cigonya and deposit 17 from Punta Esquitxador).

In two sites (Barranc de Binigaus and deposit 17 from Punta Esquitxador) it was necessary the use of acetic acid for separating the bones from the matrix. Specimens of *H. onicensis* and *H. morpheus* are housed in Institut Català de Paleontologia Miquel Crusafont (ICP, Sabadell, Spain), while those of *H. eliomyoides* and *Hypnomys* sp. are stored in the paleontological collection of one of the authors (JQ).

3.2. Body mass

High body size variation is observed between the five studied deposits. As a consequence of these differences, the body mass of each deposit was estimated in order to compare the allometric changes of each studied population. The body masses were estimated from the low tooth row length (LTRL), following the equation $\ln(\text{body mass}) = -0.6196 + 2.7020\,\ln(\text{LTRL})$ (Hopkins, 2008) (Table 1).

3.3. Measurements of postcranial bones

Functional lengths and sagittal diameters of femur, tibia, humerus and ulna were measured following the criteria of Bou (1988) (Fig. 2). A digital caliper with an error margin of ± 0.02 mm was used. Graphics that relate lengths and sagittal diameters were carried out using only complete bones, which allows us to measure both parameters simultaneously.

3.4. Diagrams

The regression models (Figs. 3–6), allometric relationships among body mass and skeletal dimensions (functional length *versus* sagittal diameter), were created following the criteria and data published in Bou et al. (1987: Table 2, p. 116). These models were constructed with a total of 46 species of insectivores, elephant shrews and rodents included in the families Chrysochloridae (2 species), Erinaceidae (2 species), Soricidae (5 species), Talpidae (2 species), Macroscelidae (2 species), Sciuridae (5 species), Geomyidae (1 species), Castoridae (2 species), Cricetidae (4 species), Spalacidae (1 species), Rhizomyidae (1 species), Arvicolidae (6 species), Muridae (4 species), Gliridae (2 species), Hystricidae (1 species), Caviidae (2 species), Hydrochaenidae (1 species), Dasyproctidae (2 species) and Myocastoridae (1 species), showing an important body mass variation (Bou et al., 1987: figs. 2, 4, 6 and 8). The relative position of *Hypnomys* spp. in the regression models is compared with *E. quecinus*. Diagrams axes are in log 10 scale, lineal measurements in centimeters and body masses in grams.

3.5. Similarity matrix of Bou

Method based on the allometric proportions (functional length *versus* sagittal diameter) of the long bones of the limbs of some extant mammal species, of which the locomotion type is known in relation to their position respect to the different regression lines. Bou (1988) made regression models (among sagittal diameter, functional length and body mass of the femur, tibia, humerus and ulna) and a matrix with the 46 studied species (with know locomotion type). Each one of these species is located over (+), under (−) or coincided with the regression line (=). This information (locomotion type in relation to the position of the species on the regression line) was recorded in a simplified matrix (Bou, 1988, Table 10) where each locomotion type is characterized by 12 symbols (+, − or =), representing each of the studied morphological

Table 1
Body mass approximations for the five studied populations.
Tableau 1
Approximations de la masse corporelle pour les cinq populations étudiées.

	Length				Body mass		
Species	*n*	Max.–min.	Mean	SD	Max.–min.	Mean	SD
Hypnomys sp. 1	10	8.69–7.42	8.09	0.46	185.41–120.98	154.26	23.49
Hypnomys sp. 2	14	10.21–9.43	9.60	0.42	286.61–187.14	243.96	28.23
Hypnomys eliomyoides	10	7.76–6.80	7.32	0.25	136.55–95.57	117.27	10.96
Hypnomys onicensis	5	7.85–7.45	7.68	0.17	140.87–122.31	133.18	8.01
Hypnomys morpheus	37	8.41–6.38	7.72	0.33	169.71–80.45	135.27	14.84

ln(body mass) = –0.6196 + 2.7020 ln(LTRL) (lower tooth row length). SD: standard deviation; Max.: maximum; Min.: minimum.

traits (three different regression models by the four limbs' long bones). The locomotion type of an extinct species is established by Bou (1988) from the similarity degree (as a percentage) among the 12 symbols that characterize each locomotion type and the symbols of the extinct species.

4. Main results

The study of the allometric changes offers high homogenous results for the samples from Menorca and Mallorca (Table 2). We have not found remarkable differences between functional length and sagittal diameter of the femur, tibia, humerus and ulna of *Hypnomys* spp. compared with *E. quercinus* and some mainland rodents and insectivores (Figs. 3–6).

The results offered by the Bou's Similarity Matrix (Table 3) indicate that *Hypnomys* spp. and *E. quercinus* show a degree of overlapping similar (92%) to the arboreal species (Fig. 7). *Hypnomys* spp. is a 25% better adapted for the jumping and digging than *E. quercinus* and a 17% better adapted for the gliding locomotion. In regard to the walking species, *Hypnomys* spp. is (compared to *E. quercinus*) better adapted (7%) to this type of locomotion. These results (with the exception of those related with the digging locomotion) agree with the phenogram obtained by Bou (1988: fig. 26) and indicate the better adaptation of *Hypnomys* spp. for the arboreal life, given that the jumping and gliding capabilities are tightly related to the arboreal life (Bou, 1988). It seems obvious, from a taxonomical point of view, that *Hypnomys* was not a gliding species in the narrowest sense of the term. On the other hand, the greater walking capability of *Hypnomys* spp. does not necessarily involve a life habits more terrestrial, because this type of locomotion can also be related with the arboreal life style and the way how *Hypnomys* spp. dwelled in this kind of habitat.

5. Discussion

Non-cursorial mammals (as small sized rodents) are those that race only occasionally, accelerating their bodies during a short period of time. This fast acceleration entails a great energetic cost. The stylopodium of non-cursorial mammals is slightly abducted. From a postural point of view, they take up an intermediate position between cursorial animals, with slightly flexed (upright), and sprawling ones, those with highly flexed limbs (Hildebrand, 1985). Cursorial mammals are characterized by highly straight limbs, slightly or no abducted longer bones (especially metapodials and stylopodium's bones) than the non-cursorial mammals with a gravity center farther from the ground (Hildebrand, 1985).

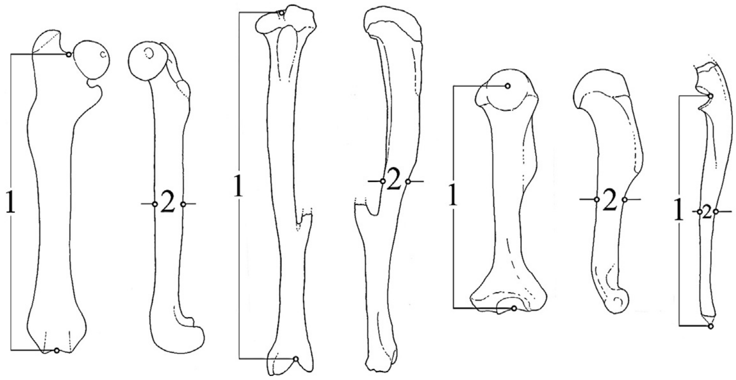

Fig. 2. Measurements of the limbs' long bones of *Hypnomys* spp. 1: functional length; 2: functional or sagittal diameter: taken at the halfway of the functional length or halfway between the articular surfaces of the proximal and distal epiphysis.

Fig. 2. Mesures des os longs des extrémités d'*Hypnomys* spp. 1 : longueur fonctionnelle ; 2 : diamètre fonctionnel ou sagittal : distance moyenne entre les surfaces articulaires de l'épiphyse proximale et distale.

Table 2
Bone measurements (mm).
Tableau 2
Mesures d'os (mm).

HUMERUS

	Length				Diameter		
Species	*n*	Max.–min.	Mean	SD	Max.–min.	Mean	SD
Hypnomys sp. 1	4	–	–	–	2.95–2.77	2.88	0.08
Hypnomys sp. 2	5/11	30.42–27.82	29.13	1.13	3.70–2.87	3.34	0.25
Hypnomys eliomyoides	2	–	–	–	2.45–2.16	2.30	0.20
Hypnomys onicensis	5/61	24.90–22.25	23.46	0.95	3.15–2.17	2.64	0.22
Hypnomys morpheus	13/27	25.06–20.11	21.98	1.35	2.87–2.10	2.50	0.20

ULNA

	Length				Diameter		
Species	*n*	Max.–min.	Mean	SD	Max.–min.	Mean	SD
Hypnomys sp. 2	3	–	–	–	3.53–2.26	2.87	0.63
Hypnomys eliomyoides	2/3	28.40–25.10	26.75	2.33	2.67–2.44	2.58	0.12
Hypnomys onicensis	4/11	27.12–23.41	25.77	1.64	2.81–2.05	2.30	0.24
Hypnomys morpheus	6	–	–	–	2.50–1,75	2.09	0.29

FEMUR

	Length				Diameter		
Species	*n*	Max.–min.	Mean	SD	Max.–min.	Mean	SD
Hypnomys sp. 1	1/3	–	29.55	–	3.33–2.57	3.04	0.41
Hypnomys sp. 2	1/6	–	38.70	–	4.01–3.46	3.79	0.23
Hypnomys eliomyoides	1/3	–	30.33	–	2.81–2.59	2.65	0.13
Hypnomys onicensis	2/40	33.11–31.61	32.36	1.06	3.19–2.18	2.73	0.18
Hypnomys morpheus	2/14	35.76–32.12	33.94	2.57	3.47–2.40	2.89	0.29

TIBIA

	Length				Diameter		
Species	*n*	Max.–min.	Mean	SD	Max.–min.	Mean	SD
Hypnomys sp. 1	5	–	–	–	2.55–2.19	2.35	0.13
Hypnomys sp. 2	1/3	–	46.47	–	2.94–2.59	2.71	0.19
Hypnomys onicensis	11	–	–	–	2.98–2.13	2.55	0.28
Hypnomys morpheus	2/4	43.92–43.91	43.92	–	2.82–1.97	2.59	0.41

SD: standard deviation; Max.: maximum; Min.: minimum

Table 3
Relative position of *Hypnomys* spp. in relation to the six different locomotion types.
Tableau 3
Position relative de *Hypnomys* spp. par rapport aux six types différents de locomotion.

	Humerus			Ulna			Femur			Tibia		
	D/L	BM/L	BM/D	D/L	BM/L	BM/D	D/L	BM/L	BM/D	D/L	BM/L	BM/D
Jumping	+	+	= +	+	+	=	+	+	+	+	+	+
Arboreal	= +	+	+	+	+	–	= +	+	+	+	+	=
Gliding	+	+	+	+	+	–	+	+	+	+	+	+
Fossorial	–	–	+	–	–	+	–	–	–	–	–	=
Swimming	+ –	–	+ =	+	+ =	–	= –	–	–	+	+	–
Walking	+ =	= –	= +	+	+ =	– =	+	–	– +	+	+	+ –
Eliomys quercinus	=	+	= +	+	+	–	=	+	+	+	+	–
Hypnomys spp.	–	+ =	+	+	+	(∗)	+ =	+	+	+	+	+ =

(+): positive relative position (above the regression line); (–): negative relative position (below the regression line); (=): neutral relative position (coinciding with the regression line); the star (∗) indicates the coincidence of the three types of the relative positions in relation to the regression line (+ – =). *Eliomys quercinus* data comes from Bou (1988: Table 9 *D*: Sagittal diameter; *L*: functional length; BM: body mass.

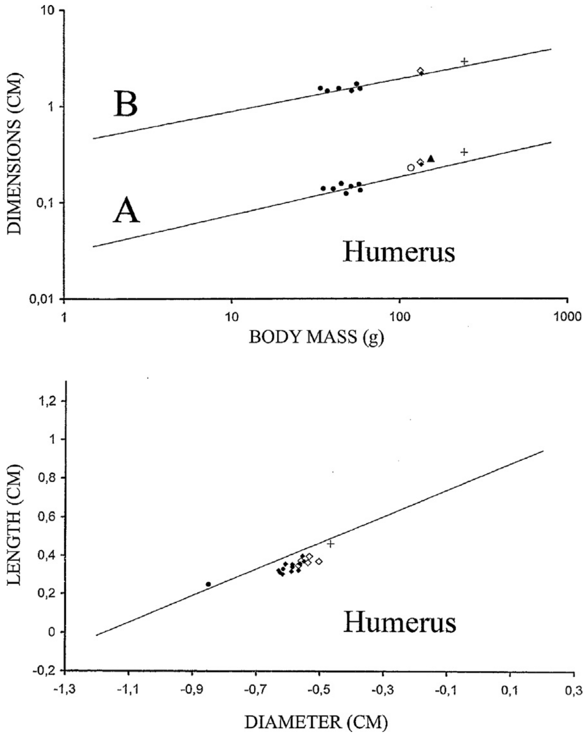

Fig. 3. Graphic representations (axes in log 10 scale) of the diameter and length (log Y = log 0.8014 + 0.7429 log X) (below) and body mass in relation to the diameter (A) (log Y = log 0.0302 + 0.3944 log X) and length (B) (log Y = log 0.4080 + 0.3377 log X) (above) of the humerus of *H. eliomyoides* (circle), *Hypnomys* sp. from Sa Cigonya (black triangle), *Hypnomys* sp. from Punta Esquitxador (cross), *H. onicensis* from Sa Pedrera de s'Ònix (big inclined white square) and *H. morpheus* from Sa Cova de sa Bassa Blanca (small inclined black square). *Eliomys quercinus* (black circle).

Fig. 3. Représentations graphiques (échelle des axes à log 10) des diamètre et longueur (log Y = log 0,8014 + 0,7429 log X) (en bas) et de la masse corporelle, en relation avec le diamètre (A) (log Y = log 0,0302 + 0,3944 log X) et la longueur (B) (log Y = log 0,4080 + 0,3377 log X) (en haut) de l'humérus d'*H. eliomyoides* (cercle), *Hypnomys* sp. de Sa Cigonya (triangle noir), *Hypnomys* sp. de Punta Esquitxador (croix), *H. onicensis* de Sa Pedrera de s'Ònix (grand carré blanc incliné) et *H. morpheus* de Sa Cova de sa Bassa Blanca (petit carré noir incliné). *Eliomys quercinus* (cercle noir).

After Bou (1988).

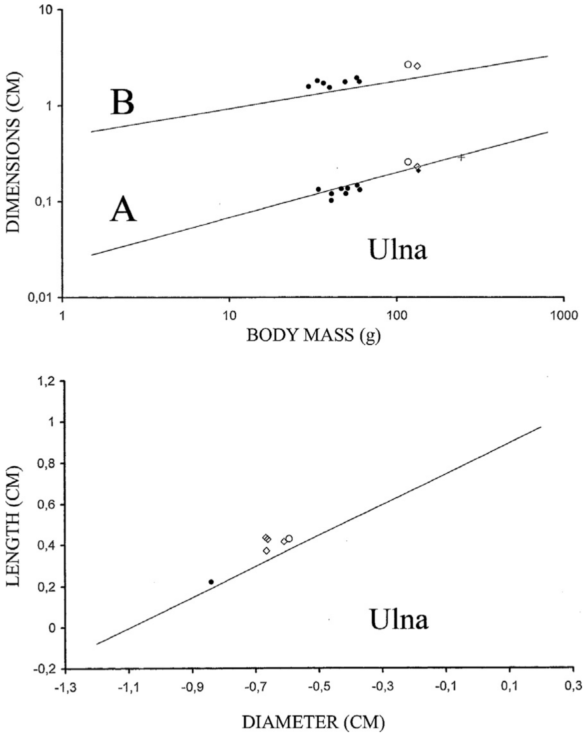

Fig. 4. Graphic representations (axes in log 10 scale) of the diameter and length (log Y = log 0.8176 + 0.7477 log X) (below) and body mass in relation to the diameter (A) (log Y = log 0.0236 + 0.4646 log X) and length (B) (log Y = log 0.4814 + 0.2862 log X) (above) of the ulna of *H. eliomyoides* (circle), *Hypnomys* sp. from Punta Esquitxador (cross), *H. onicensis* from Sa Pedrera de s'Ònix (big inclined white square) and *H. morpheus* from Sa Cova de sa Bassa Blanca (small inclined black square). *Eliomys quercinus* (black circle).

Fig. 4. Représentations graphiques (échelle des axes à log 10) des diamètre et longueur (log Y = log 0,8176 + 0,7477 log X) (en bas) et la masse corporelle, en relation avec le diamètre (A) (log Y = log 0,0236 + 0,4646 log X) et la longueur (B) (log Y = log 0,4814 + 0,2862 log X) (en haut) du cubitus d'*H. eliomyoides* (cercle), *Hypnomys* sp. de Punta Esquitxador (croix), *H. onicensis* de Sa Pedrera de s'Ònix (grand carré blanc incliné) et *H. morpheus* de Sa Cova de sa Bassa Blanca (petit carré noir incliné). *Eliomys quercinus* (cercle noir).

After Bou (1988).

The obtained results of the tibia's and ulna's functional length of *Hypnomys* spp. do not coincide with the analysis realized by Bover et al. (2010) from an unique individual (Bover et al., 2010: table S6), who observed a lengthening of the zeugopodium bones. Bover et al. (2010) documented the first case of limbs' lengthening in a Balearic Neogene endemic vertebrate. Our results do not confirm this.

The body reconstruction of *H.* cf. *onicensis* and *H. morpheus* (Bover et al., 2010; figs. 6 and 7) shows a specimen with less flexed limbs than *E. quercinus*. Concerning this, the more terrestrial life style and the limbs' lengthening emphasized by Bover et al. (2010) implies important postural and locomotion modifications in these two species. These traits seem to be more appropriate of a cursorial mammal than of a typical insular one. In an insular environment, where trophic resources are more limited and lower predation pressure exists, the lengthening and less flexion of the limbs are not the optimal solution from an energetic and postural point of view (Biewener, 1990; Van der Geer et al., 2010: p. 361).

Regarding this, the evolutionary trends of two typical insular mammals as *M. balearicus* and *N. rex* point in opposite direction. In other words, in both cases it is observed that there is a reduction of the limbs length and an approach of the body gravity center to the ground. Locomotion of *M. balearicus* and *N. rex* is slower, more stable and powerful than that of their mainland ancestors (Quintana et al., 2011; Sondaar, 1977). From this point of view, the evolutionary trends observed in these two mammals are clearly different from those of *Hypnomys*. In this case no remarkable allometric changes are related with functional lengths and sagittal diameters of the limbs' long bones. Limbs proportions (and the arboreal life style) of *Hypnomys* spp. could be explained, in part, by the birds of prey's pressure, whose existence is well-documented in the Pliocene

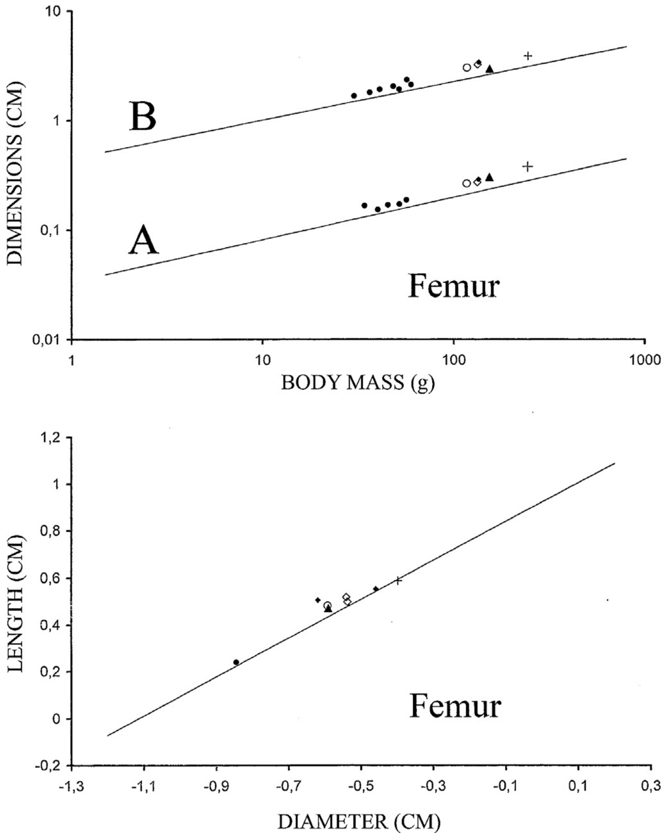

Fig. 5. Graphic representations (axes in log 10 scale) of the diameter and the length (log Y = log 0.9230 + 0.8279 log X) (below) and body mass in relation to the diameter (A) (log Y = log 0.0341 + 0.3847 log X) and length (B) (log Y = log 0.4491 + 0.3517 log X) (above) of the femur of *H. eliomyoides* (circle), *Hypnomys* sp. from Sa Cigonya (triangle), *Hypnomys* sp. from Punta Esquitxador (cross), *H. onicensis* from Sa Pedrera de s'Ònix (big inclined white square) and *H. morpheus* from Sa Cova de sa Bassa Blanca (small inclined black square). *Eliomys quercinus* (black circle).

Fig. 5. Représentations graphiques (échelle des axes à log 10) des diamètre et longueur (log Y = log 0,9230 + 0,8279 log X) (en bas) et de la masse corporelle, en relation avec le diamètre (A) (log Y = log 0,0341 + 0,3847 log X) et la longueur (B) (log Y = log 0,4491 + 0,3517 log X) (en haut) du fémur d'*H. eliomyoides* (cercle), *Hypnomys* sp. de Sa Cigonya (triangle), *Hypnomys* sp. de Punta Esquitxador (croix), *H. onicensis* de Sa Pedrera de s'Ònix (grand carré blanc incliné) et *H. morpheus* de Sa Cova de sa Bassa Blanca (petit carré noir incliné). *Eliomys quercinus* (cercle noir).

After Bou (1988).

and Pleistocene of the Balearic archipelago (Seguí, 1998). Despite this, the total stress balance would be lesser than that from the mainland, bone histology results of *Hypnomys* disclose a delay of the maturation and a higher expectancy (9 years) compared with *E. quercinus* (García-Martínez et al., 2011).

Conclusions of Bover et al. (2010) about locomotion of *Hypnomys* spp. overestimate the degree of terrestriality in front of the arboreal aptitudes of *H.* cf. *onicensis* and *H. morpheus*, although a low probability percentage was obtained by Bover et al. (2010) for this kind of locomotion (P = 3.3%) in comparison to the arboreal one (P = 74.6%).

The analysis by Bover et al. (2010) also includes data about the extant populations of *E. quercinus* from the Balearic Islands (Formentera and Mallorca-Menorca), characterized by significant differences in body size as a consequence of a supposed insular differentiation. Those differences are used (in a subtle way) to establish a correlation between the increase of body size and their more terrestrial life style, as it occurs, presumably, in *H.* cf. *onicensis* and *H. morpheus*. Correlation between body size and locomotion (supported by the factorial discriminant analysis) disagrees with the fact that extant populations of *E. quercinus* from the Balearic Islands are related with relatively recent introductions from mainland populations with several origins, but with similar locomotion aptitudes. According to Alcover (1988a,b) and Moreno (2002), Formentera's population forms part of the *lusitanicus* group, distributed in the South-West of the Iberian Peninsula and characterized by a large size, while populations from Mallorca and Menorca would form part of the *quercinus* group, characterized by individuals of less size that would take up an important part of the Iberian Peninsula. Thus in this case, the discriminant analysis would not be useful to verify supposed "insular divergences" (Bover et al., 2010), but it seems to confirm different geographical origins of the Balearic populations of *E. quercinus*.

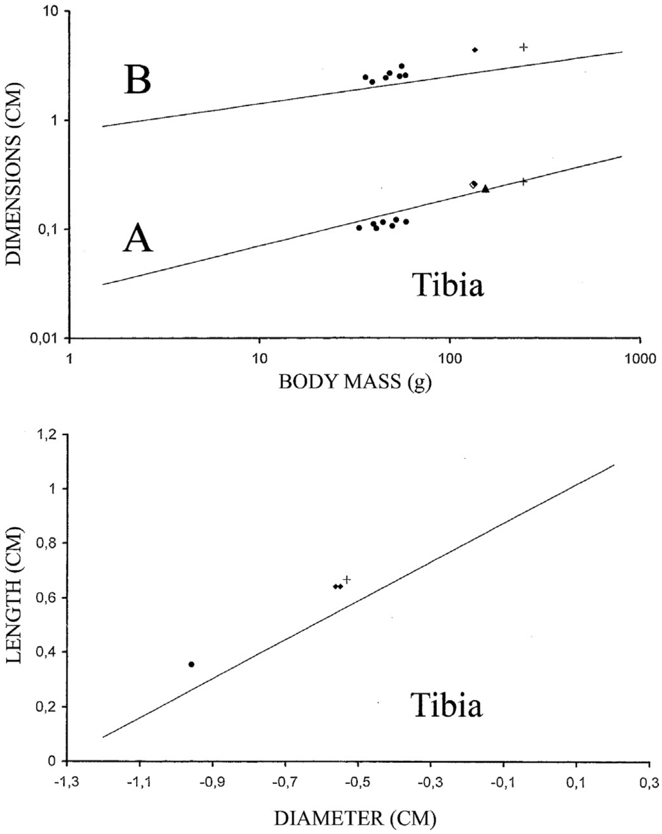

Fig. 6. Graphic representations (axes in log 10 scale) of the diameter and length (log Y = log 0.9464 + 0.7145 log X) (below) and body mass in relation to the diameter (A) (log Y = log 0.0266 + 0.4268 log X) and length (B) (log Y = log 0.7969 + 0.2489 log X) (above) of the tibia of *Hypnomys* sp. from Sa Cigonya (black triangle), *Hypnomys* sp. from Punta Esquitxador (cross), *H. onicensis* from Sa Pedrera de s'Ònix (big inclined white square) and *H. morpheus* from Sa Cova de sa Bassa Blanca (small inclined black square). *E. quercinus* (black circle).

Fig. 6. Représentations graphiques (échelle des axes à log 10) des diamètre et longueur (log Y = log 0,9464 + 0,7145 log X) (en bas) et de la masse corporelle, en relation avec le diamètre (A) (log Y = log 0,0266 + 0,4268 log X) et la longueur (B) (log Y = log 0,7969 + 0,2489 log X) (en haut) du tibia à *Hypnomys* sp. de Sa Cigonya (triangle noir), *Hypnomys* sp. de Punta Esquitxador (croix), *H. onicensis* de Sa Pedrera de s'Ònix (grand carré blanc incliné) et *H. morpheus* de Sa Cova de sa Bassa Blanca (petit carré noir incliné). *Eliomys quercinus* (cercle noir).

After Bou (1988).

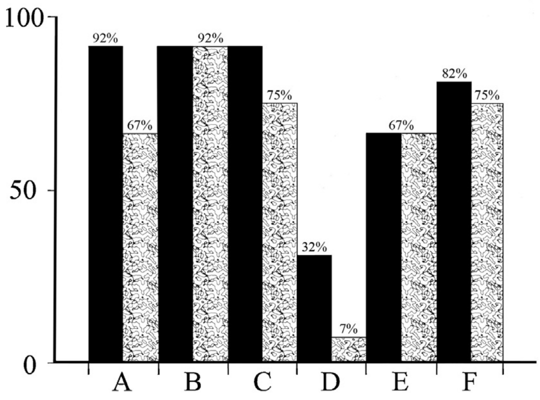

Fig. 7. Similarity percentages of locomotion types in *Hypnomys* spp. (vertical black bars) compared with *Eliomys quercinus* (vertical white bars). A. Jumping. B. Arboreal. C. Gliding. D. Fossorial. E. Swimming. F. Walking.

Fig. 7. Pourcentages de similitude des types de locomotion chez *Hypnomys* spp. (barres noires verticales), en comparaison avec *Eliomys quercinus* (barres blanches verticales). A. Saut. B. Locomotion de type arboricole. C. Glisse. D. Creusement. E. Nage. F. Marche.

6. Conclusions

The study of the allometric changes regarding the functional length and sagittal diameter of the femur, tibia, humerus and ulna shows that proportions of *Hypnomys* spp. are similar to *E. quercinus*.

Taken together, the results of the Similarity Matrix of Bou indicate a clear predominance of the arboreal locomotion for *Hypnomys* spp. and more developed digging skills than *E. quercinus*. Some results obtained by Bover et al. (2010) point to the same direction. However, these authors give, surprisingly, greater weight to the terrestrial locomotion, although it has a low probability. The absence of allometric changes in the length of the limbs' long bones observed in our analysis are in contradiction to the results of Bover et al. (2010). Our results would be related with the existence of woodlands on the Balearic Islands during the Neogene (Alcover et al., 2000; Bauzà, 1971; Colom, 1978; López de Heredia et al., 2005; Pérez-Obiol et al., 1996).

The results of the proportions of limbs' long bones of *Hypnomys* spp. are interesting, considering that some of them (greater width of the distal humerus) (Bover et al., 2010) are congruent with the observations of other larger insular mammals (*M. balearicus* and *N. rex*) (Alcover et al., 1981; Quintana, 2005). On the other hand, *Hypnomys* spp. does not show significant allometric changes of the relative proportions of functional length and sagittal diameter of the limbs' long bones. It is likely that differences of the relative length of the limbs' long bones between *Hypnomys* spp. and *N. rex*/*M. balearicus* would be related to their body size and the probability to be hunted by birds of prey. The absence of significant allometric changes in relative length of the limbs' long bones would be the evolutionary response to predation in *Hypnomys* spp. The absence or the low predation pressure on *N. rex* and *M. balearicus* caused some of their locomotion trends and triggered some significant allometric changes. Although it is true that the morpho-skeletal traits of the mainland ancestor of *Hypnomys* spp. are unknown, it is possible that the existence of a supposed "conservative" corporal proportions (related to arboreal locomotion) with other "innovative" tendencies (related to more developed digging skills) are associated, to a certain extent, with the environmental stress exercised by birds of prey. Perhaps, this type of predation stopped certain skeletal changes (significative variation in the length of the limbs' long bones), but it did not prevent the promotion of the ethological traits related to the digging and the enlargement of the ecological niche, because, as it has been mentioned before, the environmental stress assessment was lesser than that from the mainland.

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