Mandible Morphometrics, Dental Microwear Pattern, and Paleobiology of the Extinct Balearic Dormouse Hypnomys morpheus

Authors: Hautier, Lionel, Bover, Pere, Alcover, Josep Antoni, and Michaux, Jacques

Mandible morphometrics, dental microwear pattern, and palaeobiology of the extinct Balearic Dormouse *Hypnomys morpheus*

LIONEL HAUTIER, PERE BOVER, JOSEP ANTONI ALCOVER, and JACQUES MICHAUX

Hypnomys morpheus is a giant endemic dormouse from the Pleistocene deposits of Mallorca and Menorca (Balearic Islands, Spain). The present paper aims to interpret the morphological divergence between the mandibles of *Hypnomys* and of its extant relative *Eliomys*, the outline of the mandible being used as a marker of the morphological divergence. By comparison with the mandible of *Eliomys*, the more massive mandible of *Hypnomys* has recorded an ecological shift of the insular lineage towards a more abrasive diet, including hard vegetable matter, and a different niche. A microwear analysis of the teeth of *Hypnomys* was simultaneously performed as it can shed light on the diet, and is independent from the comparison of the mandibles. *Hypnomys* possibly ate harder food items than *Eliomys*, and likely occupied most of the island environments. *Hypnomys* appears to have differentiated from its ancestral type toward a more generalized morphology because of the lack of competitors.

Key words: Mammalia, Rodentia, Gliridae, *Hypnomys morpheus*, Fourier analysis, microwear, morphological evolution, paleodiet, Balearic Islands, Spain.

Lionel Hautier [Lionel.Hautier@univ-montp2.fr], Laboratoire de Paléontologie, Institut des Sciences de l'Evolution, Université de Montpellier 2, UMR-CNRS 5554, CC 064; 2, Place Eugène Bataillon, F-34095 Montpellier Cedex 5, France;
Pere Bover[pbover@amnh.org], Department of Mammalogy, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA;
Josep Antoni Alcover [vieapba@uib.es], Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Cta de Valldemossa km 7,5, 07122 Palma de Mallorca, Balearic Islands, Spain;
Jacques Michaux [michaux@isem.univ-montp2.fr], Laboratoire EPHE de Paléontologie des Vertébrés, et Institut des Sciences de l'Evolution, Université de Montpellier 2, UMR-CNRS 5554, CC 064; 2, Place Eugène Bataillon, F-34095 Montpellier Cedex 5, France.

Introduction

Isolation on islands is a factor well-known to induce evolutionary changes, and a rather frequent event is the origination of giant forms in small mammals like rodents. The Pleistocene deposits of Mallorca and Menorca (Balearic Islands, Spain) provide a good case study. They yielded a peculiar mammalian fauna including the giant dormouse *Hypnomys* (e.g., Bate 1919; De Bruijn 1966; Mills 1976), a rodent of the family Gliridae, the closest relative of which is considered to be the extant garden dormouse *Eliomys* (McKenna and Bell 1997). A recent review of the vertebrate fauna from the Balearic Islands (Bover et al. 2008) sheds new light on the context of *Hypnomys* evolutionary history. The genus *Hypnomys* includes three species in Mallorca: *Hypnomys waldreni* Reumer, 1979 from the late Pliocene, *H. onicensis* Reumer, 1994 from the late Pliocene–early Pleistocene boundary and *H. morpheus* Bate, 1919 from the middle and late Pleistocene and Holocene. In Menorca, *H. morpheus* has been recorded, and two other species of unclear status

(Reumer 1982, 1994) have also been described, *H. mahonensis* Bate, 1919 and *H. eliomyoides* Agusti, 1980. A fourth species has been considered in Mallorca from the early Pliocene, but with no specific assignment (*Hypnomys* sp.). In Eivissa a species of *Hypnomys* was found in the late Pliocene deposit of Cova de ca na Reia, but as with the fourth species of Mallorca, no specific assignment has been proposed. Another species, *H. gollcheri* de Bruijn, 1966 from Malta deposits, was at one time considered. For Storch (1974), *H. gollcheri* and *Leithia cartei* Adams, 1867 are probably synonymous taxa, but Zammit-Maempel and De Bruijn (1982) included it in *Maltamys*. *Hypnomys* sp. was also cited from Nuraghe Su Casteddu in Sardinia (Esu and Kotsakis 1980), but later emended to *Tyrrhenoglis* (e.g., Kotsakis 2003). So *Hypnomys* is restricted to the Balearic Islands and only *H. morpheus* has a very rich fossil record. In the late Pleistocene, this species was only found associated with two other endemic species: *Nesiotites hidalgo* Bate, 1945 (Soricidae; Bate 1945) and *Myotragus balearicus* Bate, 1909 (Caprinae; Bate 1909), a poorly diversified fauna as frequently found on
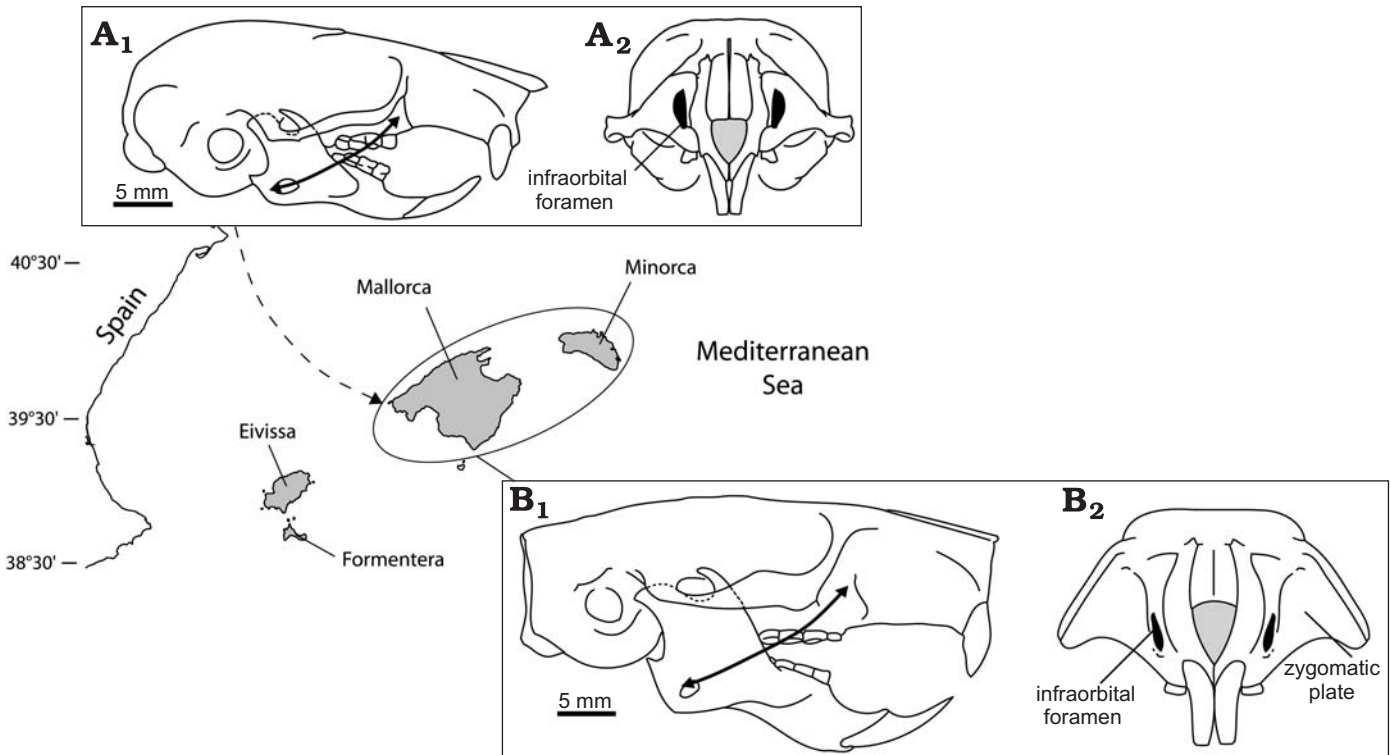
Acta Palaeontol. Pol. 54 (2): 181–194, 2009

DOI: 10.4202/app.2008.0001

Fig. 1. Zygomasseteric construction in Balearic dormice. **A**. Skull of extant *Eliomys quercinus ophiusae* (MNHN1983-832) in lateral (A_1) and anterior (A_2) views. **B**. Skull of *Hypnomys morpheus* in lateral (B_1) and anterior (B_2) views. Arrows show the origin and the insertion of the lateral portions of the masseter. The skull of *Hypnomys morpheus* (**B**) corresponds to a reconstruction. *Eliomys* and *Hypnomys* are represented at the same scale. The map summarizes the evolutionary history of Balearic glirids—*Hypnomys* is a lineage derived from an *Eliomys* species isolated by the sea level rise that followed the Messinian salinity crisis, then *Eliomys quercinus ophiusae* followed the first human colonization (dashed arrow represents a hypothetical pathway of colonization).

islands. Man colonized Mallorca probably between 2350 and 2150 cal BC (Alcover 2008; Bover et al. 2007), the last documentation of the three endemic mammals postdating 3650 cal BC (*Myotragus*), 3030 cal BC (*Nesiotites*) and 4840 cal BC (*Hypnomys*) (Bover and Alcover 2003; Bover and Alcover 2007). Since the endemic fauna is considered to have become extinct before 2350 cal BC, it can be assumed that humans cohabited for some time with these three endemic species and that the latter rapidly became extinct (Bover and Alcover 2007). However, humans were not the sole invaders at the end of the Pleistocene: *Eliomys* and *Apodemus*, then *Mus* and *Rattus*, also settled on the Balearic Islands.

Since *Hypnomys* and *Eliomys* are phylogenetically very close, *Hypnomys* represents an insular lineage derived from an *Eliomys* species isolated on the Balearic Islands by the sea level rise that followed the Messinian salinity crisis (Fig. 1; Bover et al. 2008). According to Mills (1976: 36), *Hypnomys* exhibits many "characters in common with less advanced glirids" such as a U-shaped coronal suture, lingulate interparietal, diffuse supra-occipital process, converging jugals, diverging upper cheek teeth alveoli, the form of the zygo-squamosal process and its anterior extension, the form of the bulla, position of the "ectopterygoid" foramina, extension of lateral pterygoid process, a small or occluded maxillary fora-

men, the relative size of the iliac surface, a large terminal phalanx of the first toe and the overall robustness of the mandible. Considering the dental pattern, Zammit-Maempel and de Bruijn (1982) and Holden (2005) suggested to include *Hypnomys* within *Eliomys*. However, *H. morpheus* depicts an original zygomasseteric construction (Fig. 1), in which the zygomatic arch was strong indicating that the lateral masseter muscle was highly developed and anchored on a wide zygomatic plate. Among traits to be considered is the relatively small-sized infraorbital foramen, through which the medial masseter passes. Such an arrangement is unique among extant and extinct glirids, the lateral masseter evolving in *Hypnomys* toward a sciuromorphous-like condition (Fig. $1B_1$). These diagnostic traits justify referring the insular species to a distinct genus derived from *Eliomys*. Regardless, *H. morpheus* appears distinct from any *Eliomys* species and a comparison of this insular form with the latters may shed light on the evolution under isolation. Moreover, *Eliomys* is unique among extant glirids by being clearly partially insectivorous and a predator of molluscs, insect larvae and occasionally even of small mammals (Ognev 1963). Considering that interspecific interactions, primarily competition, might be the driving force behind this evolutionary specialisation, we investigate whether an absence of congeners would lead to the evolution of morphology. It can be consequently ex-

pected that any departure of *H. morpheus* from such a diet must be easy to recognize, using extant glirids as reference.

The precise comparison given by Mills (1976) will be considered using the mandible as a proxy, the hypothesis being that there must be changes in mandible shape correlative to the changes in morphology of the zygomatic plate (Hautier et al. 2008). As a matter of fact, the study of the mandible is easier compared to the study of the skull due to the two dimensional structure of the dentary bone and the number of complete lower jaws of *Hypnomys* at our disposal. In addition, many studies have shown that the mandible provides good information both on change of size as well as changes in shape (Angerbjörn 1986; Renaud and Millien 2001; Michaux et al. 2002; Renaud and Michaux 2003). The present study also aims at testing the conclusion of the mandible shape analysis using data provided by a microwear analysis of the molars, with each component of the masticatory apparatus showing characteristics that may reflect one parameter of the species niche, i.e., the diet. We investigated whether *Hypnomys* occurring on Balearic Islands in an impoverished insular fauna reversed the evolutionary direction of *Eliomys* lineages. For *Hypnomys* that evolved with few or no competitors, we predict that changes in habitat use would lead to the evolution of a more generalist morphology. This case will not only show how a lineage could modify its habitat use under isolation, but it may also provide clues to its extinction.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; IMEDEA, Institut Mediterrani d'Estudis Avançats, Palma de Mallorca, Spain; MNHN, Museum National d'Histoire Naturelle, Paris, France; UMC, Montpellier University Collection.

Other abbreviations.—EFT, Elliptic Fourier Transform; FDA, Factorial Discriminant Analysis; PCA, Principal Component Analyses; RFT, Radial Fourier Transform; Nfp, number of fine pits; Nfs, number of fine scratches; Nlp, number of large pits; Np, total number of pits; Ns, total number of scratches; Nws, number of wide scratches.

Material and methods

For morphometric analyses, studied specimens come from the collection of the MNHN (collection Vertébrés supérieurs Mammifères et Oiseaux), the collection of the Department of Mammalogy of the AMNH, and the collection of the IMEDEA. We analysed 124 glirid mandibles of both sexes, representing 4 species of 3 different genera: *Hypnomys morpheus* (fossil specimens from holocene deposits of Balearic islands), *Eliomys quercinus* (fossil specimens from holocene deposits of Balearic islands and extant insular and continental representatives), *E. melanurus* and *Dryomys nitedula*. In order to reduce the intraspecific effects related to allometric changes, only adult specimens showing the third molar erupted were considered in the analysis.

The material used for the microwear analysis belongs to the collection of the IMEDEA. Two species and 37 specimens were included: 24 extinct *Hypnomys morpheus* from Mallorca and 13 extant *Eliomys quercinus ophiusae* from Formentera. Many altered specimens were rejected from analysis because of post-mortem deterioration (Andrews 1990; King et al. 1999). *Dryomys nitedula* was not included in this analysis because the current analysis techniques cannot deal with very small teeth. The list of measured individuals is given in the Appendix 5.

Mandible outline.—Two morphometric methods are commonly used for describing the morphology of rodent mandibles: landmarks and outline analyses (Bookstein 1991; Foote 1989). However, the simple morphology of the mammalian mandible requires the digitalization of type 2 landmarks (i.e., points of maximum curvature along the outline), which are more sensitive to certain errors in their location than points defined with bone sutures. In this context, we decided to quantify the shape of mandibles using outline analyses based on the Fourier method (Renaud and Michaux 2003; Michaux et al. 2007), because outlines give access to features involved in the insertion for masticatory muscles. The outline corresponds to a two-dimensional projection of the vestibular side of the mandible (Renaud and Michaux 2003). As teeth were often missing, only the outline of the dentary was considered. Left mandibles only were measured. If the left mandibles were broken, mirror images of the right ones were computed. The starting point of the outline was chosen at the antero-dorsal edge of the incisor alveolus and for each mandible 64 points at equally spaced intervals along the outline were recorded (Renaud and Michaux 2003).

Two Fourier methods are commonly used: the Radial Fourier Transform (RFT) and the Elliptic Fourier Transform (EFT). Here, we applied the Elliptic Fourier Transform, a method allowing a description of complex outlines (Kuhl and Giardina 1982). This method is based on the separate Fourier decompositions of the incremental changes of the x- and y- coordinates as a function of the cumulative length along the outline (Kuhl and Giardina 1982). Thus, the outline is approximated by a sum of trigonometric functions of decreasing wavelength (i.e., the harmonics). Any harmonic corresponds to four coefficients: A_n, B_n for x, and C_n, D_n for y, defining an ellipse in the xy-plane. The coefficients of the first harmonic, describing the best-fitting ellipse of any outline, are used to standardize both the size and orientation of the mandible. After standardization, these coefficients correspond to the residuals, and are not considered in the following statistical analyses (Crampton 1995; Renaud et al. 1996).

An advantage of the EFT method is that if the wavelength of the harmonic is low, more substantial details of the morphology of the mandibles can be considered. Given that the measurement noise increases with the rank of the harmonics, the rank of the last one was empirically determined as the coefficient of variation of the harmonic ampli-

tude (i.e., the square root of the sum of the squared Fourier coefficients; Renaud et al. 1996) of repeated measurements of five specimens. As shown in previous works (e.g., Renaud and Michaux 2003), the first seven harmonics offer a good compromise between measurement error, information content and numbers of variables to consider. Following inverse processes [Inverse Fourier transform method (Rohlf and Archie 1984)] the coefficients of Fourier allow us to reconstruct the mandible outline and to visualize the shape changes.

Statistical procedures were performed with R1.5.0 (Ihaka and Gentleman 1996). For each outline, 24 coefficients comprising seven harmonics (EFT_7) were considered. The intraspecific shape variation was compared with the interspecific one with Multivariate analyses of variance (Manova) on these Fourier coefficients, using the species as a factor (Claude et al. 2003). A multivariate regression of the Fourier coefficients on size, estimated by the square root of the outline area (Michaux et al. 2007), permitted us to assess the effect of allometric variation on the overall shape of the mandible. The morphological variability of extant glirids was quantified with a principal component analyses (PCA). Extinct taxa were then added as supplementary data. Because our data set consisted of a relatively large number of variables, the shape space was simplified to the first Principal Components (the number of PCs was defined in order to keep 98% of the interspecific shape variance). Manova in association with a test of significance (Wilk's Lambda test) was performed on these PCs in order to assess the effects of phylogeny (i.e., subspecies assignments) and geographical range. A Factorial Discriminant Analysis (FDA) of shape coordinates was performed to assess if there was a discrimination of the mandible outline with the geographic range.

Microwear analysis.—Microwear features are generated on enamel dental facets during the course of mastication (Walker et al. 1978; Solounias and Hayek 1993). Recent studies (e.g., Solounias and Semprebon 2002; Merceron et al. 2004a; Nelson et al. 2005) showed that the diet of extinct species might be deduced from the dental microwear pattern, especially the number of pits (semi-circular scars) and scratches (elongated scars). Although tooth microwear has been widely studied in fossil and extant ungulate species (e.g., Solounias and Semprebon 2002; Merceron et al. 2004a), it has been also considered as a good indicator of diet in other taxa such as rodents (Nelson et al. 2005). The orientation of the scratches is also usually considered to identify the direction of jaw movement during chewing (Charles et al. 2007). Forty molars were selected for this microwear analysis. Only teeth of *Hypnomys* in association with a mandible were taken into consideration. Microwear was measured on the protoconid and the hypoconid of lower second molars (M_2) for both modern glirid species and *Hypnomys*. We decided to choose the protoconid and the hypoconid because they provided a large and flat occlusal surface which con-
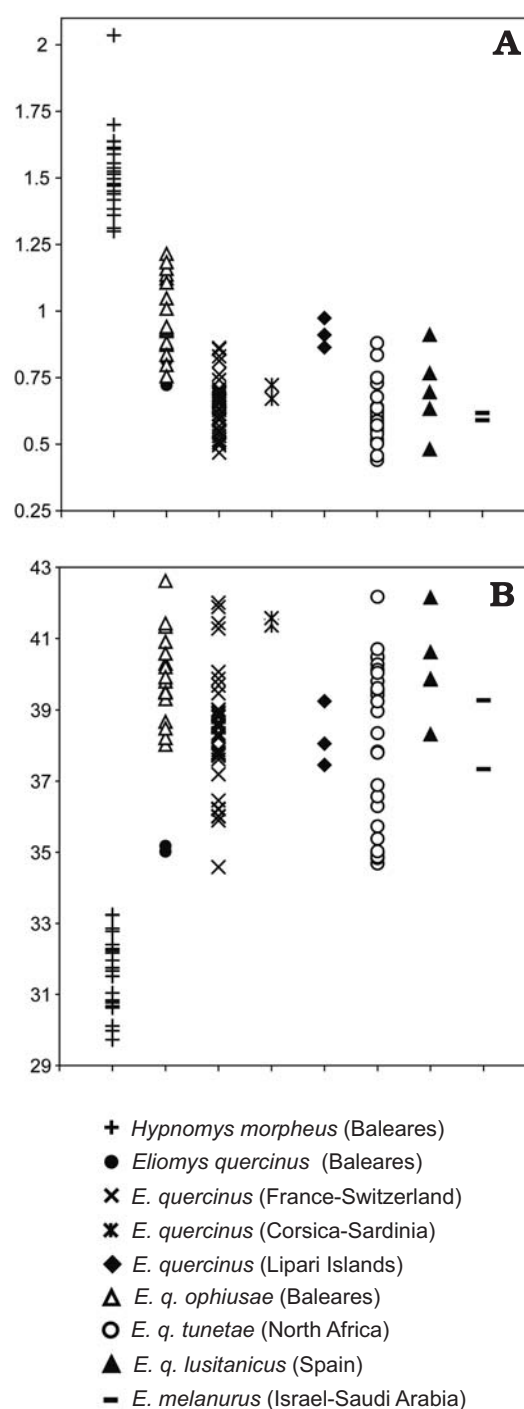
Fig. 2. Distribution of the area (**A**) and circularity (**B**) of the mandibles of *Hypnomys* and *Eliomys*.

trasts with the morphology of all other cuspids of the glirid tooth that merge into crests.

The teeth were carefully cleaned using acetone and cotton swabs. Microwear was measured on translucid casts made using polyvinylsiloxane (Coltene President Microsystem®) and transparent epoxin resin (In Epox®, ADAM Montparnasse) left to cure for one day. For this study, dental facets were digitized using a ZEISS® SV11 M2B with the ×115 ob-

Fig. 3. Shape differentiation of the mandible on the first two axes of the Principal Components Analysis (PCA) performed on Fourier coefficients of the mandibles. Outlines are reconstructed on the 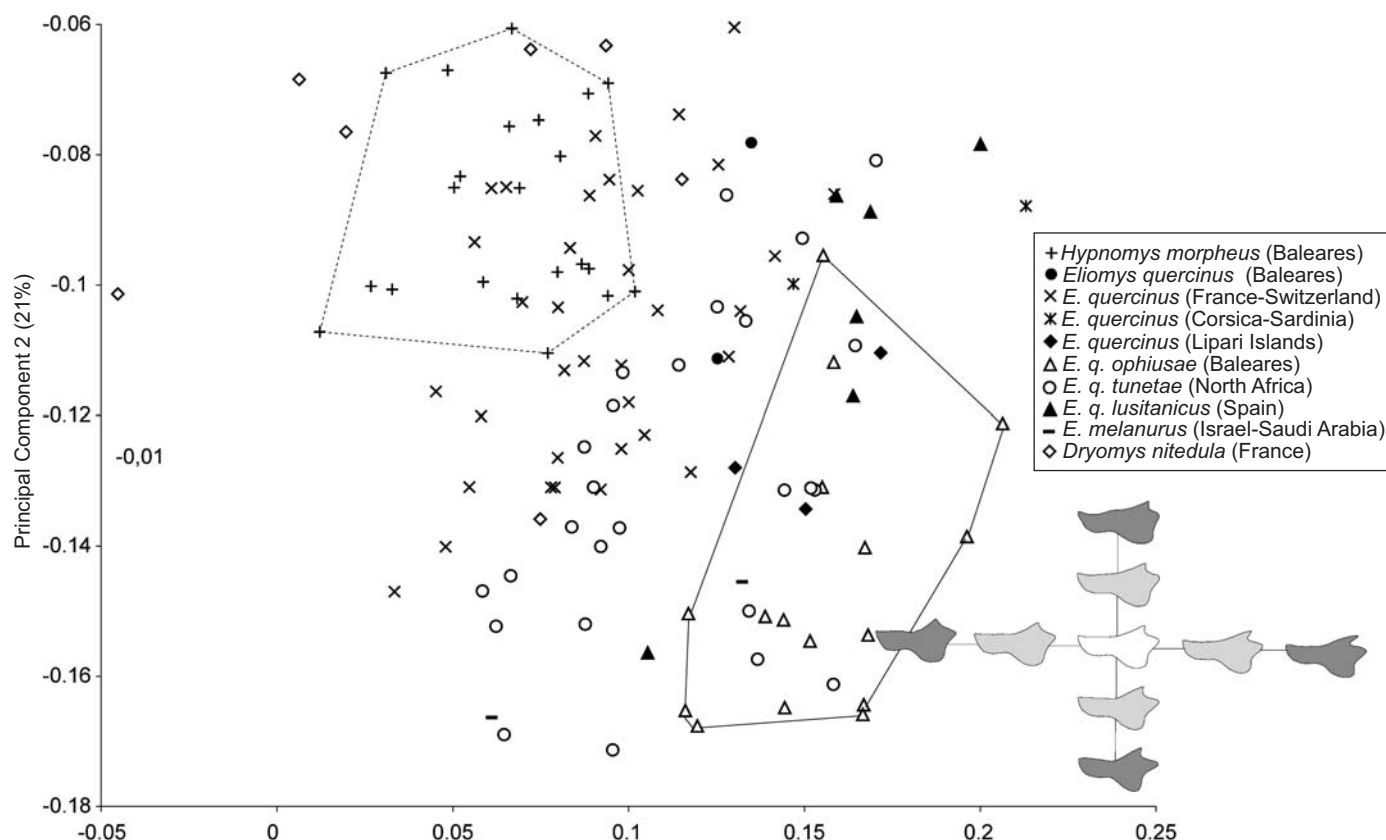first two canonical axes, the light grey outline represents the maximum values of the axes, and the dark grey outline corresponds to extreme reconstruction.

jective and transmitted-light through the stereomicroscope. This method is cheaper, simpler and totally non-invasive (no need for coating) compared to methods using a scanning electron microscope (SEM; Hayek et al. 1992; Solounias et al. 1988). Then, a $0.01 mm^2$ area was delimited on each facet to take variations in dental microwear patterns along molar facets into consideration (Gordon 1982). Dental microwear is quantified using Optimas® (v.6.5.2) software (Media Cybernetics®).

We documented four microwear variables: the total number of scratches (Ns), the total number of pits (Np), the number of wide scratches (Nws) and the number of large pits (Nlp). Two supplementary variables can be deduced from them: the number of fine scratches (Nfs) and the number of fine pits (Nfp). The value of 5 μm for scratch width or pit diameter discriminates fine scratches or pits from wide ones. Scratches were distinguished from pits using the minor/major axis ratio. The pits have a ratio higher than 1/4, whereas scratches have a lower one (Grine 1986). Four variables were integrated in the multivariate analyses: the total number of scratches (Ns), the number of wide scratches (Nws), the total number of pits (Np) and the number of large pits (Nlp). Statistical procedures were performed with R1.5.0 (Ihaka and Gentleman 1996). A probability level of 0.05 was assumed for all tests.

Results

Mandible outline.—The mandible of *Hypnomys* is always bigger than the mandible of all other glirids here studied (Fig. 2A). The circularity (Fig. 2B) corresponds to the ratio of perimeter length squared by the area, as calculated with Optimas®. In fact, the circularity of the mandible gives an estimation of its compactness or roundness that is related to the degree of relative differentiation of its processes. Compared to extant glirids, *Hypnomys* shows low values of circularity and is characterized by a mandible with a high and large ascending ramus and more weakly differentiated processes. In our dataset, *Hypnomys* is clearly individualized by the overall massivity of its mandible, as it was observed by Mills (1976).

The intraspecific variation of the shape is obviously less important than the interspecific variation (Wilk's Lambda test: Value = 0.0634, F = 10.73, p < 0.001) and does not significantly contribute to the shape differentiation. Manovas on PCs_{1-12} indicated a significant morphological differentiation of the mandible outline within the dataset involving phylogeny (i.e., subspecies, Wilk's Lambda test: Value = 0.0134, F = 7.43, p< 0.001). Respectively, 46.8% and 21% of among-group variance is explained by PC1 and PC2 (Fig. 3). The mandibles of *Hypnomys* are distinct from the
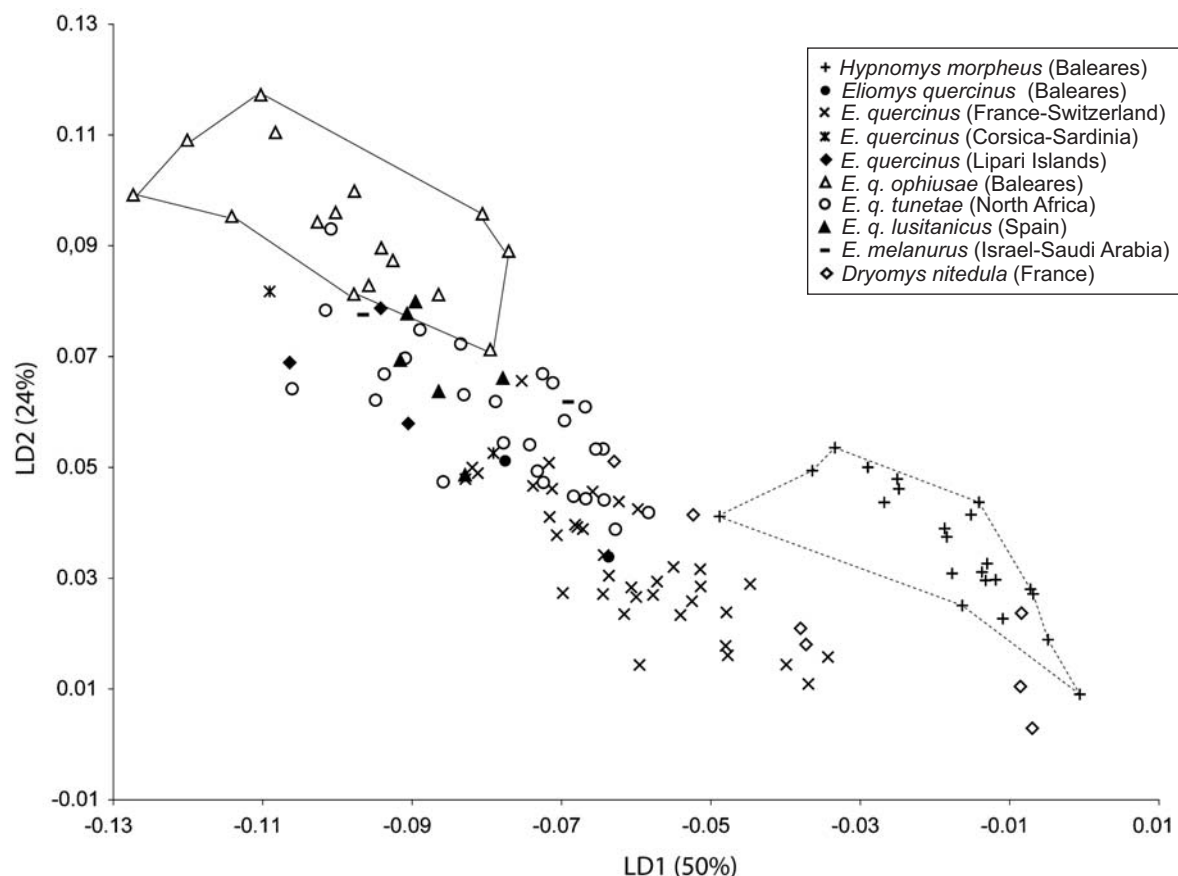
Fig. 4. Plot of the discriminant analysis of the shape coordinates (the first twelve PCS, i.e., 98% of the interspecific shape variance) versus geographic range.

mandibles of *Eliomys* regarding the first component, which appears highly correlated to the size of the coronoid and condylar processes, the individualization of the angular one, and an overall robustness of the ascending ramus. The second axis includes components related to the orientation of the coronoid and condylar processes. However, these axes are weakly informative regarding the shape variation in relation with the phylogeny (Fig. 3), and the genera *Hypnomys* and *Dryomys* remain very close to *Eliomys* in the morphological space.

A factorial discriminant analysis allowed a complete discrimination for the geographical range (Fig. 4). Manovas on PCs_{1-12} indicated a significant morphological differentiation of the mandible outline within the dataset involving geographical range (Wilk's Lambda test: Value = 0.6501, F = 3.77, p < 0.001). Mandible morphologies related to clades are significantly different and the mandible of *Hypnomys* and *Dryomys* are discriminated from the mandibles of *Eliomys* on the first discriminant axis. Mahalanobis distances (Appendix 1) indicated that the morphology of the mandible of *Hypnomys* is more similar to that of *Dryomys* (d [*Hypnomys–Dryomys*] = 75.5) than to that of *Eliomys* (d [*Hypnomys–Eliomys*] = 90.7). Although high variability is known to be an important feature in fossil island mammals, the mandibles of *Eliomys* present a high morphological variation compared to that of *Hypnomys* and *Dryomys*. This variability could be ex-

plained by the heterogeneity of the *Eliomys* sample, which includes continental and insular populations. The outline of the mandible allowed us to distinguish the continental representatives of the genus *Eliomys* from the insular ones (i.e., Balearic Islands, Lipari, Corsica and Sardinia; Fig. 4). The isolation of the latter in the shape space confirmed an insular divergence involving the morphology of the mandible. Nevertheless, they remained close to the representatives from Spain, North Africa, Israel and Saudi Arabia on the first and second discriminant axes. *E. quercinus* and *E. q. ophiusae* of Balearic Islands were associated in the shape space with *E. quercinus* of North Africa and E. *quercinus lusitanicus* of Spain, respectively.

The multivariate regression of the Fourier coefficients on size, estimated by the square root of the outline area, was highly significant (p < 0.001). Thus, allometry plays an important role for determining the pattern of morphological diversification. The size was compared to the main morphological differentiation displayed on PC1 to visualize this allometric effect (Fig. 5). Among the extant glirid sample, size and shape of the mandible are highly correlated (R = 0.46, p < 0.001). It appears that *H. morpheus* does not lie on the same allometric trajectory.

Microwear analysis.—The numbers of scratches and pits observed in all studied specimens are listed in Appendix 2.
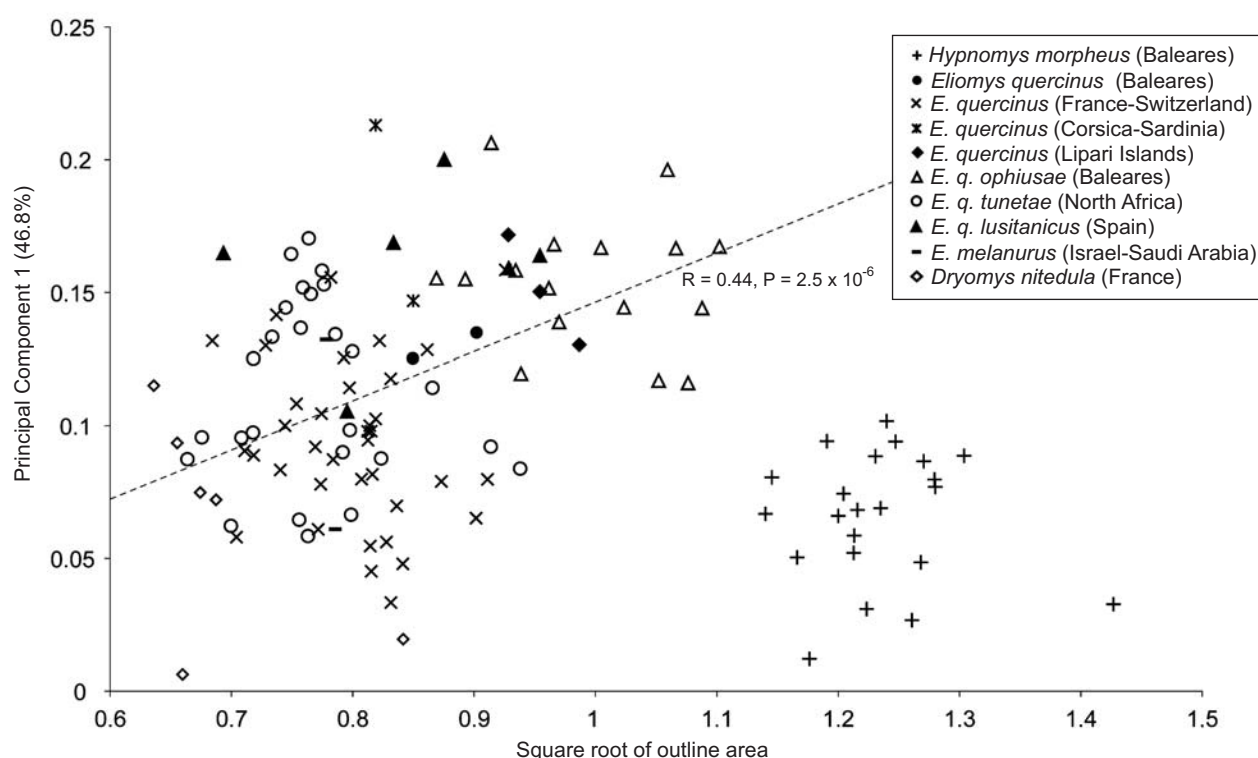
Fig. 5. Allometric relationship between the size (estimated from the square root of outline area) and the main shape signal (scores on the first principal components). The dashed line represents the linear regression between both variables for all extant glirids.

The Student tests (Appendix 3) on microwear features of both protoconid and hypoconid are not significant ($p > 0.05$), and these facets present similar microwear patterns. The total number of scratches and pits, associated to percentiles of each feature, yield information about the main characteristics of the microwear patterns. Manovas were performed on the four microwear variables (Nfs, Nws, Nfp, Nlp) measured on the protoconid and the hypoconid of the M_2 of *Hypnomys* and *Eliomys* (Table 1). They indicate significant differences ($p < 0.05$) between microwear patterns exhibited by the two genera. In terms of the average number of scratches and pits (Appendix 2), *Hypnomys* exhibits a greater range of differences than *Eliomys*. Considering the standard deviation (Appendix 4), it appears that intraspecific variation is more important in *Hypnomys* than in *Eliomys*. The latter is always characterized by a low number of scratches (Ns < 15). On the contrary, the number of scratches, especially fine ones, is very variable in *Hypnomys*. It results from univariate tests (Table 2) that the differentiation of *Hypnomys* is principally due to differences in the number of fine scratches (Nfs).

Discussion

The mandible.—Compared to *Eliomys*, *Hypnomys morpheus* is clearly a giant dormouse (Fig. 2A). An increase in size also affected insular *Eliomys*. With the exception of the continental Spanish specimens, mainland specimens of *Elio-*

Table 1. Multivariate analyses of variance (Manova) with effect species on four microwear variables: the number of fine scratches (Nfs), the number of wide scratches (Nws), the number of fine pits (Nfp) and the number of large pits (Nlp).

	Effect	Test	Value	F	dl	*p*
Hypoconid	species	wilk	0.58	4.61	25.00	0.01
Protoconid	species	wilk	0.40	4.83	13.00	0.01

Table 2. Univariate analyses of variance (Anova) on four microwear variables (Nfs, Nws, Nfp, Nlp) with effect species for the hypoconid and the protoconid.

	Effect	dl	ls F	fs *p*	ls F	ls *p*	fp F	fp *p*	lp F	lp *p*
Hypoconid	species	1	16.88	0.00	0.38	0.54	2.78	0.11	1.25	0.27
Protoconid	species	1	18.93	0.00	7.0	0.02	1.53	0.23	1.54	0.23

mys of our sample always have smaller mandibles than insular ones. Although some specimens from Mallorca are obviously larger than mainland ones, *E. quercinus* individuals living on the biggest islands (i.e., Corsica and Sardinia) are similar in size to mainland forms. These results are consistent with previous works (Angerbjörn 1986; Michaux et al. 2002; Renaud and Michaux 2003) indicating a much more complex determinism of size in insular species that depends on several combined factors like the area of the island and the presence of predators (Michaux et al. 2002; Millien 2004). In their detailed study on adaptive trends in the mandible of *Apodemus* wood mice, Renaud and Michaux (2003) identified a random shape differentiation on some islands. In our analysis, the genus *Eliomys* depicts a different case of differentiation, all the insular forms of the genus being associated on the first and second discriminant axes (Fig. 4). Concerning shape differentiation in the evolution of the Balearic glirids (i.e., *H. morpheus* and *E. quercinus ophiusae*), the the first two principal components show two distinct shifts (Fig. 3). A dorsoventral expansion of the ascending ramus and a reduced coronoid process characterize the mandible of *Hypnomys* whereas all insular forms of *Eliomys* mandibles are dorsoventrally compressed and have a well developed coronoid process distally positioned. For Satoh (1997), an increasing weight of the mandible implies an increase of the area of insertion of the masticatory muscles (especially the masseter). Thus, differences in size could be responsible for the shape differentiation. However, we showed (Fig. 5) that *H. morpheus* did not lie on the same allometric trajectory than extant *Eliomys*. If this divergence in mandibular shape cannot be explained by a simple allometric relationship, other factors (e.g., ecological factors) may play an important role in shaping the mandible.

The shape and size differentiation of the mandibles of *H. morpheus* could be related to a way of life different from that of *Eliomys*. The dorso-ventrally compressed mandible of *Eliomys* does not contradict a partially insectivorous diet (Ognev 1963; Storch 1978). Shearing meat or crushing insects requires less occlusal pressure than grinding plants or seeds (Satoh and Iwaku 2006). On the contrary, a strong incisal bite is required to kill insects or small vertebrates and the development of mandibular processes in *Eliomys* could provide a high lever advantage. Dental characters, like the high concavity of the occlusal surface of the cheek teeth (Freudenthal and Martín-Suárez 2007) underscore an adaptation towards a more insectivorous diet. In the shape space, the morphology of the outline of the mandibles of *H. morpheus* is clearly distinct from that of *Eliomys* and remains close to that of *Dryomys nitedula* a glirid more omnivorous than *Eliomys* (Grzimek 1975). The diet of *Dryomys* consists of seeds, acorns, buds, fruits, and occasionally insects, eggs and small vertebrates (Grzimek 1975). The more massive mandible of *H. morpheus* likely indicates an omnivorous species that included also very hard items (i.e., acorns, nuts, fruit) in its diet as a function of habitat and season. The masseteric arrangement (see Fig. 1), associated with the
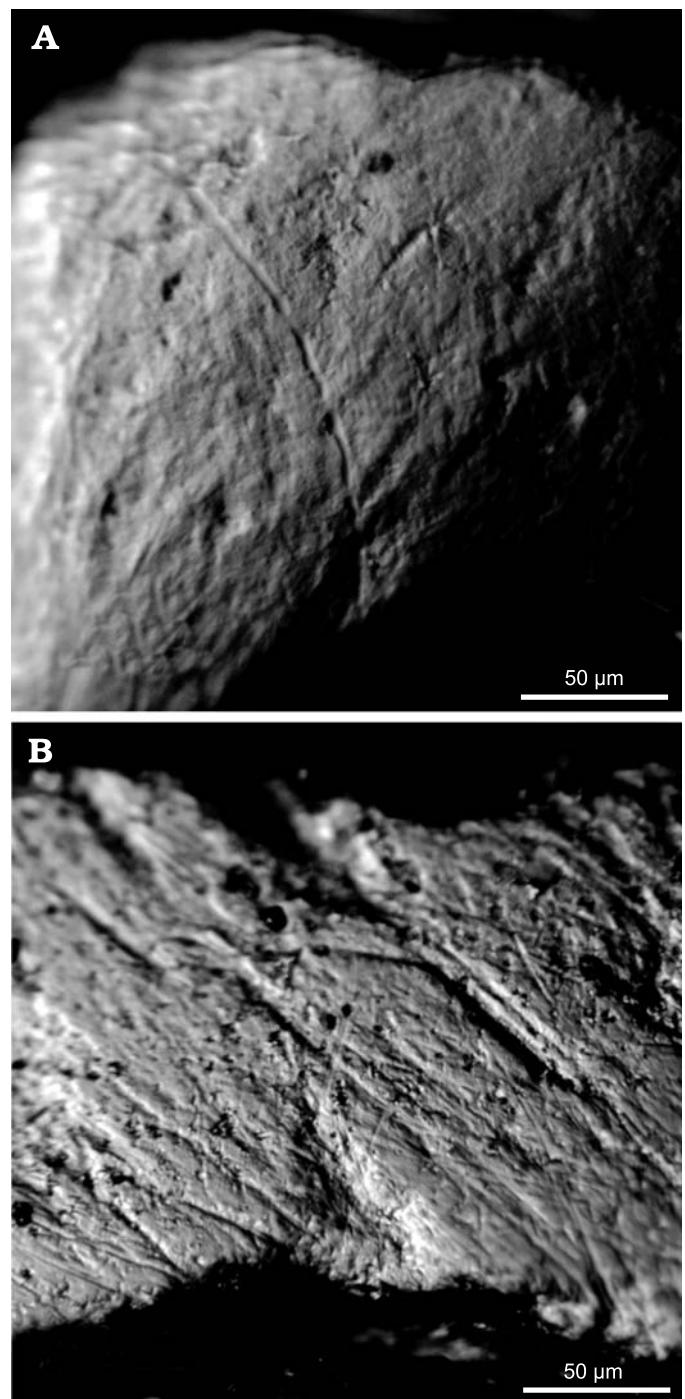
Fig. 6. Digitized photographs of the protoconid of the second molars. **A**. *Eliomys quercinus ophiusae* (IMEDEA 7357), Formentera, Balearic Islands; extant specimen. **B**. *Hypnomys morpheus* (IMEDEA 63839), Cova Estreta, Pollença, Mallorca, Holocene. Note the higher number of fine scratches in *Hypnomys*.

overall robustness of the skull and the mandible of *H. morpheus* as underlined by Mills (1976), is also consistent with our hypothesis. The differences observed between the shape differentiation of the mandible of *Eliomys* and *Hypnomys* might be related to their different evolutionary history. *H. morpheus* evolved without competition prior to the arrival of

humans and their domestic livestock. Its size increased and it adapted to a widened niche including harder food. On the contrary, *E. quercinus ophiusae* cohabited with other introduced rodents (like *Apodemus, Mus, Rattus*) and kept its initial adaptation. This explains both morphological divergences observed on the Balearic Islands.

The cheek teeth.—The microwear analysis may allow an independent assessment of this interpretation of the diet of *H. morpheus*. The dental microwear patterns of extant species depend on the food items that were consumed just before the death of the animals (e.g., Solounias et al. 1988; Teaford and Oyen 1989; Fortelius and Solounias 2000; Merceron et al. 2004a, b, 2005). The grazing species present a lower percentage of pits than the browsing ones. The statistical analysis indicates that extant *Eliomys quercinus ophiusae* and *Hypnomys morpheus* differ significantly in the number of scratches. Like other glirids, *E. quercinus ophiusae* is largely omnivorous but with a great tendency to eat eggs, insects and small vertebrates. In fact, *Eliomys* is the most carnivorous glirid currently known (Ognev 1963). The dental microwear pattern of the omnivorous-insectivorous *E. quercinus ophiusae* (Fig. 6A) is in accordance with a diet dominated by hard food items. The specimens analysed display a large percentage of pits, especially wide ones, and large scratches. Such a microwear pattern could be explained by a diet mainly composed of insects. Kahmann and Thoms (1972) recorded a highly insectivorous diet for *E. q. ophiusae* during some seasons. A similar microwear pattern, characterized by a higher number of pits and a high frequency of large pits and scratches, is also found in ground squirrels (Nelson et al. 2005). This microwear pattern was related to an abrasive diet composed by seeds and insects and the presence of more grit in the food items. For Strait (1993), fruit-eaters could present a similar dental microwear pattern and we must take this into account for the dietary reconstruction of extinct species. However, Nelson et al. (2005) showed that the omnivorous ground squirrels differed from the frugivorous tree squirrels by a higher number of pits.

The microwear pattern of *H. morpheus* (Fig. 6B) is more variable than that of *E. quercinus ophiusae*. The important intraspecific variation of the microwear pattern of *Hypnomys* could attest that it was able to adapt its diet to the seasons. This suggests a more omnivorous diet than that of *E. quercinus ophiusae*. The specimens always display larger percentages of scratches, especially fine ones, than Recent glirids do. The abundance of fine scratches suggests that *H. morpheus* could be able to eat graminoids, despite the fact that the presence of earthworms (and snails) in the diet could also explain some narrow scratches (Silcox and Tedford 2002). Fine scratches likely have an ambiguous meaning. All the specimens of *H. morpheus* show a high number of pits and large pits, which indicates the intake of hard particles (insects, worms, fruit, and graminoids). An incorporation of grit into the diet could also explain a high frequency of coarse features (Solounias and Semprebon

2002). These features were observed in species living in dry habitats (camel, pronghorn) and in species feeding on roots (bush pig). This could attest that *H. morpheus* was more terrestrial than arboreal, supporting Mills (1976). Finally, it seems that *H. morpheus* had a mixed diet. By extension, we can suppose that, being the sole omnivorous mammal of its size on the island it was able to adapt to a great number of habitats.

Conclusions

Geometric morphometrics of the mandible, as well as microwear analysis of the teeth bring new insights on the extinct dormouse *Hypnomys* from Mallorca and Menorca (Balearic Islands). The special features of *Hypnomys* already described by Mills (1976) are correlated to a massive mandible and a tooth microwear pattern characterized by a high number of fine scratches. No insular populations of *Eliomys* display such trends in their mandible morphology and tooth microwear pattern. By comparison with the European garden dormouse *Eliomys*, these traits can be interpreted for *Hypnomys* as indicating an omnivorous diet. *Hypnomys* was likely a large omnivorous glirid able to eat hard food items that may have even included graminoids. These results are also consistent with the interpretation of Mills (1976) who suggested that *H. morpheus* was terrestrial rather than arboreal. The evolutionary divergence of *Hypnomys* from *Eliomys* could be due to the fact that the *Hypnomys* lineage evolved within a highly impoverished fauna among which it was the sole rodent. *Hypnomys* that had access to diverse food resources rapidly became an endangered species when its natural environment was altered by the settlement of the first human populations and their domestic livestock.

Acknowledgements

References

Andrews, P. 1990. *Owls, Caves and Fossils*. 231 pp. University of Chicago Press, Chicago.

Angerbjörn, A. 1986. Gigantism in island populations of wood mice (*Apodemus*) in Europe. *Oikos* 47: 47–56.

Alcover, J.A. 2008. The first Mallorcans: prehistoric colonization in the Western Mediterranean. *Journal of World Prehistory* 21: 19–84.

Bate, D.M.A. 1909. Preliminary note on a new artiodactyle from Mallorca *Myotragus balearicus*, gen. et sp. nov. *Geological Magazine,* decade 5, 6: 385–389.

Bate, D.M.A. 1919. On a new genus of extinct Muscardine Rodent from Balearic Islands. *Proceedings of the Zoological Society of London* 1918: 209–222.

Bate, D.M.A. 1945. Pleistocene shrews from the larger Western Mediterranean islands. *Annals and Magazine of Natural History,* decade 11, 11: 738–769.

Bookstein, F.L. 1991. *Morphometric tools for landmark data: Geometry and Biology*. 435 pp. Cambridge University Press, Cambridge.

Bover, P. and Alcover, J.A. 2003. Understanding late Quaternary extinctions: the case of *Myotragus balearicus* (Bate, 1909). *Journal of Biogeography* 30: 771–781.

Bover, P. and Alcover, J.A. 2007. Extinction of the autochthonous small mammals from Mallorca (Gymnesic Islands, Western Mediterranean Sea) and its ecological consequences. *Journal of Biogeography* 35: 1112–1122.

Bover, P., Quintanab, J., and Alcover, J.A. 2008. Three islands, three worlds: paleogeography and evolution of the vertebrate fauna from the Balearic Islands. *Quaternary International* 182: 135–144.

Charles, C., Jaeger, J.J., Michaux, J., and Viriot, L. 2007. Dental microwear in relation to changes in the direction of mastication during the evolution of Myodonta (Rodentia, Mammalia). *Naturwissenschaften* 94: 71–75.

Claude, J., Paradis, E., Tong, H., and Auffray, J.C. 2003. A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution of the turtle shell. *Biological Journal of the Linnean Society* 79: 485–501.

Crampton, J.S. 1995. Elliptic Fourier shape analysis of fossil bivalves: some practical considerations. *Lethaia* 28: 179–186.

De Bruijn, H. 1966. On the Pleistocene Gliridae (Mammalia, Rodentia) from Malta and Mallorca. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen ser. B* 78: 480–496.

Esu, D. and Kotsakis, T. 1980. Presenza di *Hypnomys* Bate (Gliridae, Rodentia) nel Villafranchiano di Nuraghe Su Casteddu (Nuoro, Sardegna). *Rendiconti dell'Accademia Nazionale dei Lincei ser. 8* 68: 123–127.

Foote, M. 1989. Perimeter-based Fourier analysis: a new morphometric method applied to the trilobite cranidium. *Journal of Paleontology* 63: 880–885.

Fortelius, M. and Solounias, N. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301: 1–36.

Freudenthal, M. and Martín-Suárez, E. 2007. An index for concavity of the occlusal surface of the cheek teeth and an assessment of concavity in Gliridae (Mammalia, Rodentia). *Palaeontologia Electronica* 10: 9A: 1–24. http://palaeo-electronica.org/paleo2007_2/00122/index.html.

Gordon, K. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. *American Journal of Physical Anthropology* 59: 195–215.

Grine, F.E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *Journal of Human Evolution* 15: 783–822.

Grzimek, B. 1975. *Grzimek's Animal Life Encyclopaedia,Vols. 10–13, Mammals, I–IV*. 657 pp. Van Nostrand Reinhold, New York.

Hautier, L., Michaux, J., Marivaux, L., and Vianey-Liaud, M. 2008. The evolution of the zygomasseteric construction in Rodentia, as revealed by a geometric morphometric analysis of the mandible of *Graphiurus* (Rodentia, Gliridae). *Zoological Journal of the Linnean Society* 154: 807–821.

Hayek, C.L.A., Bernor, R.L., Solounias, N., and Steigerwald, P. 1992. Preliminary studies of Hipparionine horse diet as measured by tooth microwear. *Annales Zoologici Fennici* 28: 187–200.

Holden, M.E. 2005. Family Gliridae. *In*: D.E. Wilson and D.M. Reeder (eds.), *Mammals Species of the World, a Taxonomic and Geographic Reference*, 3rd ed., 819–841, Smithsonian Institution Press, Washington.

Ihaka, R. and Gentleman, R. 1996. R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5: 299–314.

Kahmann, H. and Thoms, G. 1972 Der Gartenschläfer *Eliomys quercinus ophiusae* Thomas, 1925 von der Pityuseninsel Formentera (Lebensführung). *Veröffentlichungen der Zoologischen Staatssammlung München* 16: 29–49.

King, T., Andrews, P., and Boz, B. 1999. Effect of taphonomic processes on dental micro-wear. *American Journal of Physical Anthropology* 108: 359–373.

Kotsakis, T. 2003. Fossil glirids of Italy: the state of the art. *Coloquios de Paleontología*, volume extraordinaire 1: 335–343.

Kuhl, F.P. and Giardina C.R. 1982. Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* 18: 259–278.

McKenna M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.

Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., and Heintz, E. 2004a. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207: 143–163.

Merceron, G., Viriot, L., and Blondel, C. 2004b. Tooth microwear pattern in roe deer (*Capreolus capreolus*, L.) from Chizé (Western France) and relation to food composition. *Small Ruminant Research* 53:125–132.

Merceron, G., Bonis, L. de, Viriot, L., and Blondel, C. 2005. Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in eastern Mediterranean during the Messinian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 217: 173–185.

Michaux, J.R., Goüy de Bellocq, J., Sara, M., and Morand, S. 2002. Body size increase in rodent populations: a role for predators. *Global Ecology and Biogeography* 11: 427–436.

Michaux, J., Chevret, P., and Renaud, S. 2007. Morphological diversity of Old World rats and mice (Rodentia, Muridae) mandible in relation with phylogeny and adaptation. *Journal of Zoological Systematics and Evolutionary Research* 45: 263–279.

Millien, V. 2004. Relative effects of climatic changes, isolation and competition on body size evolution in the Japanese field mouse, *Apodemus argenteus*. *Journal of Biogeography* 31: 1267–1276.

Mills, D.H. 1976. Osteological study of the Pleistocene dormouse *Hypnomys morpheus* Bate from Mallorca (Rodentia, Gliridae). *Publications from the Palaeontological Institution of the University of Uppsala* 4: 4–57.

Nelson, S., Badgley, C., and Zakem, E. 2005. Microwear in modern squirrels in relation to diet. *Palaeontologia Electronica* 8: 14A: 15. http://palaeo-electronica.org/paleo2005_1/nelson14/issue1_05.html.

Ognev, S. 1963. *Mammals of the U.S.S.R. and Adjacent Countries, Vol. 6 Rodents*. 330 pp. Israel Program for Scientific Translations, Jerusalem.

Renaud. S., Michaux, J., Jaeger, J.J., and Auffray, J.C. 1996. Fourier analysis applied to *Stephanomys* (Rodentia, Muridae) molars: non progressive evolutionary pattern in gradual lineage. *Paleobiology* 22: 255–265.

Renaud, S. and Millien, V. 2001. Intra- and interspecific morphological variation in the field mouse species *Apodemus argenteus* and *A. speciosus* in the Japanese archipelago: the role of insular isolation and biogeographic gradients. *Biological Journal of the Linnean Society* 74: 557–569.

Renaud, S. and Michaux, J. 2003. Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice. *Journal of Biogeography* 30: 1–12.

Reumer, J.W.F. 1982. Some remarks on the fossil vertebrates from Menorca, Spain. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen ser. B* 85: 77–87.

Reumer, J.W.F. 1994. *Eliomys* (*Hypnomys*) *onicensis* nomen novum, to replace the homonym *Hypnomys intermedius* Reumer 1981 (Rodentia: Gliridae) from Mallorca. *Zeitschrift für Säugetierkunde* 59: 380–381.

Rolph, F.J. and Archie, J.W. 1984. A comparison of Fourier methods for the description of wing shape in Mosquitoes (Diptera: Culicidae). *Systematic Zoology* 33: 302–317.

Satoh, K. 1997. Comparative functional morphology of mandibular forward movement during mastication of two murid rodents, *Apodemus speciosus* (Murinae) and *Clethrionomys rufocanus* (Arvicolinae). *Journal of Morphology* 231: 131–142.

Satoh, K. and Iwaku, F. 2006. Jaw muscle functional anatomy in northern grasshopper mouse, *Onychomys leucogaster*, a carnivorous murid. *Journal of Morphology* 267: 987–999.

Silcox, M.T. and Teaford, M.F. 2002. The diet of worms: an analysis of mole dental microwear. *Journal of Mammalogy* 83: 804–814.

Solounias, N., Teaford, M.F., and Walker, A. 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology* 14: 287–300.

Solounias, N. and Hayek, C.L.A. 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. *Journal of Zoology* 229: 421–445.

Solounias, N. and Semprebon, G. 2002. Advances in the reconstruction of ungulates ecomorphology with application to early fossil equids. *American Museum Novitates* 3366: 1–49.

Storch, G. 1974. Quartäre Fledermaus-Faunen von der Insel Malta. *Senckenbergiana Lethaea* 55: 407–434.

Storch, G. 1978. Familie Gliridae Thomas, 1987 – Schläfer. *In*: J. Niethammer and F. Krapp (eds.), *Handbuch der Säugetiere Europas 1, Rodentia I*, 201–280, Akademische Verlaggesellschaft, Wiesbaden.

Strait, S.G. 1993. Molar microwear in extant small-bodied faunivorous mammals: an analysis of feature density and pit frequency. *American Journal of Physical Anthropology* 92: 63–79.

Teaford, M.F. and Oyen, O.J. 1989. In vivo and in vitro turnover in dental microwear. *American Journal of Physical Anthropology* 80: 447–460.

Walker, A., Hoeck, H.N., and Perez, L. 1978. Microwear of Mammalian teeth as an indicator of diet. *Science* 201: 908–910.

Zammit-Maempel, G. and Bruijn de, H. 1982. The Plio-Pleistocene Gliridae from the Mediterranean islands reconsidered. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen ser B* 85: 113–128.

Appendix 1

Mahalanobis distances between the mandibles of *Hypnomys morpheus*, *Eliomys quercinus*, *Eliomys melanurus*, and *Dryomys nitedula*.

	Hypnomys morpheus	*Eliomys quercinus*	*Eliomys melanurus*	*Dryomys nitedula*
Hypnomys morpheus	–	90.7	125.3	75.5
Eliomys quercinus	90.7	–	43.5	55.3
Eliomys melanurus	125.3	43.5	–	68.1
Dryomys nitedula	75.5	55.3	68.1	–

Appendix 2

Comparison of the microwear pattern of the protoconid and the hypoconid. df, degree of freedom; N, Number of microwear variables for both the protoconid and Hypoconid; Nfp, number of fine pits; Nfs, number of fine scratches; Nlp, number of large pits; Nws, number of wide scratches; p, p value; t, t-statistic.

Species	Variables	N	df	t	p
Hypnomys morpheus	Nfs	21/10	29	-0.29	0.77
	Nws	21/10	29	-1.46	0.16
	Nfp	21/10	29	-0.85	0.40
	Nlp	21/10	29	-0.91	0.37
Eliomys quercinus ophiusae	Nfs	8/8	14	-0.67	0.52
	Nws	8/8	14	0.80	0.44
	Nfp	8/8	14	-1.58	0.14
	Nlp	8/8	14	-0.80	0.44

Appendix 3

Microwear data for *Hypnomys morpheus* (N: 24) and *Eliomys quercinus* (N: 13) from the Balearic Islands. FP, fine pits; FS, fine scratches; LP, large pits; WS, wide scratches.

A

Tooth facet	Species	Specimen no.	All scratches	All pits	Wide scratches	Large pits	% pits
Protoconid	*Eliomys quercinus ophiusae*	7383	11	24	1	2	68.6
		7371	14	24	4	7	63.2
		7369	10	18	2	4	64.3
		7369	14	46	4	11	76.7
		7351	1	20	1	5	95.2
		7323	9	35	1	5	79.5
		7357	7	37	3	3	84.1
		7388	7	16	1	2	69.6
	Hypnomys morpheus	L8	55	40	1	5	42.1
		64294	44	29	5	13	39.7
		64247	43	34	6	6	44.2
		64141	57	34	9	3	37.4
		64052	35	52	7	9	59.8
		64020	15	18	3	5	54.5
		63903	16	15	2	4	48.4
		63840	17	34	5	8	66.7
		63883	37	73	3	13	66.4
		63839	32	41	6	3	56.2
Hypoconid	*Eliomys quercinus ophiusae*	7309	7	13	3	3	65.0
		7383	5	33	1	7	86.8
		7388	9	10	5	4	52.6
		7337	5	9	0	1	64.3
		7355	9	18	5	5	66.7
		7357	14	19	3	4	57.6
		7397	7	16	3	2	69.6
		7441	13	37	2	5	74.0
	Hypnomys morpheus	63020	16	12	0	2	42.9
		63729	11	55	1	0	83.3
		63833	21	20	0	3	48.8
		63837	26	18	2	6	40.9
		63839	21	15	2	2	41.7
		63840	31	42	3	10	57.5
		63883	17	9	2	3	34.6
		63904	16	10	3	1	38.5
		63977	24	26	1	4	52.0
		63979	28	45	3	6	61.6
		64019	29	27	4	5	48.2
		64020	14	23	4	7	62.2
		64052	28	30	3	8	51.7
		64141	55	55	9	12	50.0
		64155	63	39	3	4	38.2
		64157	58	17	7	6	22.7
		64247	55	53	8	12	49.1
		64294	38	38	4	8	50.0
		64296	38	22	5	4	36.7
		64326	48	43	5	3	47.3
		64466	38	53	1	12	58.2

B

Tooth facet	Species	%FS	%WS	%FP	%LP
Protoconid	*Eliomys quercinusophiusae*	19.1	5.8	61.8	13.3
	Hypnomys morpheus	42.2	6.5	41.7	9.6
Hypoconid	*Eliomys quercinusophiusae*	21.0	9.8	55.4	13.8
	Hypnomys morpheus	45.6	5.3	40.2	8.9

Appendix 4

Mean and standard deviation of the four microwear variables (fs, ws, fp, and lp) of *Hypnomys morpheus* and *Eliomys quercinus*. Nfp, number of fine pits; Nfs, number of fine scratches; Nlp, number of large pits; Nws, number of wide scratches.

Species	Variables	Mean	sd
Hypnomys morpheus	Nfs	28.8	14.1
	Nws	3.3	2.4
	Nfp	25.4	14
	Nlp	5.6	3.6
Eliomys quercinus ophiusae	Nfs	5.9	3.2
	Nws	2.8	1.8
	Nfp	15.5	9
	Nlp	3.9	1.9

Appendix 5

List of measured specimens. Un, unnumbered specimen.

Mandible outline

Hypnomys morpheus: IMEDEA 64321, IMEDEA 64324, IMEDEA 63904, IMEDEA 63901, IMEDEA 6390, IMEDEA 64332, IMEDEA 64330, IMEDEA 64338, IMEDEA 64335, IMEDEA 63977, IMEDEA 63840, IMEDEA 63800, IMEDEA 63798, IMEDEA 63802, IMEDEA 63801, IMEDEA 63705, IMEDEA 64013, IMEDEA 64154, IMEDEA 64158, IMEDEA 64141, IMEDEA 64144, IMEDEA 64148, IMEDEA 63305, IMEDEA 63301, IMEDEA 64462, IMEDEA 64105, IMEDEA 64155

Dryomys nitedula: MNHN1911-800, MNHN1962-334, MNHN1993-411, MNHN1993-412, MNHN1995-2685, MNHN1982-501, MNHN1964-375

Eliomys quercinus: 63804, 63803, MNHN1993-2611, MNHN1993-2559, MNHN1993-2573, MNHN1993-2599, MNHN1993-2600, MNHN1993-2602, MNHN1993-2603, MNHN1993-2604, MNHN1993-2608, MNHN1993-2610, MNHN1910-16, MNHN1912-695, MNHN1983-871, MNHN1983-870, MNHN1983-869, MNHN1955-647, MNHN1911-2093, MNHN1967-1422, MNHN1983-873, MNHN1983-666, MNHN1970-251, MNHN1967-1421, MNHN1956-639, MNHN1932-4412, MNHN1957-501, MNHN1985-1042, MNHN1883-624, MNHN1908-359, MNHN1910-753, MNHN1913-234, MNHN1932-4403, MNHN1932-4404, MNHN1932-4408, MNHN1932-4410, MNHN1938-856, MNHN1942-414, MNHN1956-642, MNHN1956-643, MNHN1957-500, MNHN1957-502, MNHN1957-503, MNHN1958-227, MNHN1958-258, MNHN1958-259, MNHN1958-266, MNHN1961-739, MNHN1961-885, MNHN1962-817, MNHN1962-1816, MNHN1962-2270, MNHN1962-2275, MNHN1964-403, MNHN1966-1052, MNHN1973-781, MNHN1973-783, MNHN1973-784, MNHN1975-101, MNHN1978-134, MNHN1983-594, MNHN1983-832, MNHN1983-857, MNHN1983-858, MNHN1990-669, MNHN1990-670, MNHN1991-278, MNHN1994-1137, MNHN2006-206, MNHN1961-885, MNHN1993-2556, MNHN1993-2593, MNHN1993-2594, MNHN1993-2595, MNHN1993-2598, MNHN1993-2607, MNHN1993-2612, MNHN1993-2615

Eliomys quercinus ophiusae: IMEDEA 7353, IMEDEA 7344, IMEDEA 7340, IMEDEA 7358, IMEDEA 7345, IMEDEA 7341, IMEDEA 7343, IMEDEA 7347, IMEDEA 7355, IMEDEA 7356, IMEDEA 7354, IMEDEA 7346, MNHN1967-1420, MNHN1983-832, MNHN1967-1422, MNHN1970-251

Eliomys lusitanicus (as labelled in MNHN): MNHN1961-882, MNHN1961-883, MNHN1961-884, MNHN1966-1051

Eliomys tunetae (as labelled in MNHN): MNHN1978-133, MNHN1978-127, MNHN1978-126, MNHN1978-130, MNHN1978-133, MNHN1978-125

Eliomys melanurus: MNHN1983-873, MNHN1995-284

Microwear analysis

Hypnomys morpheus: IMEDEA 63020, IMEDEA 63729, IMEDEA 63833, IMEDEA 63837, IMEDEA 63839, IMEDEA 63840, IMEDEA 63883, IMEDEA 63904, IMEDEA 63977, IMEDEA 63979, IMEDEA 64019, IMEDEA 64020, IMEDEA 64052, IMEDEA 64141, IMEDEA 64155, IMEDEA 64157, IMEDEA 64247, IMEDEA 64294, IMEDEA 64296, IMEDEA 64326, IMEDEA 64466, IMEDEA 63903, IMEDEA L8

Eliomys quercinus ophiusae: IMEDEA 7309, IMEDEA 7383, IMEDEA 7388, IMEDEA 7337, IMEDEA 7355, IMEDEA 7357, IMEDEA 7397, IMEDEA 7441, IMEDEA 7371, IMEDEA 7369, IMEDEA 7351, IMEDEA 7323