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Morphometric and genetic structure of the edible dormouse (*Glis glis*): a consequence of forest fragmentation in Turkey

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Past climatic fluctuations influenced forest habitats and impacted heavily the distribution of forest species, such as the edible dormouse, by changing the distribution and composition of forests themselves. Such effects may be valid for ongoing climate change as well. To improve our understanding of the edible dormouse's history and how it responded to changes in its environment, we investigated its variation across the understudied zone of Northern Turkey using two complementary markers of differentiation: the mitochondrial cytochrome *b* gene for genetics, and size and shape of the first upper molar for phenotypic differences. Genetic and morphometric results were strongly discrepant. Genetic analyses evidenced an amazing homogeneity throughout the Eurasian range of the edible dormouse, whereas morphometrics pointed to a complex, step-wise differentiation along the Black Sea coast, the main signal being an opposition between Easternmost and Westernmost Turkish dormice. The genetic homogeneity suggests that this phenotypic differentiation is not the inheritance of glacial refuges, but the consequence of a more recent post-glacial isolation. The transition between the European and Asian groups is located eastwards from the Marmara straits, undermining its claimed role as an efficient barrier but stressing the importance of climatic and vegetational factors. A secondary differentiation between populations from the Central Black Sea coast and Easternmost regions was evidenced, attributed to a complex interplay of climatic, topographic, anthropogenic, and ecological factors. Turkey, at the crossroad of European and Asian species, heavily impacted by the current global change including climatic and anthropogenic factors, appears of importance for understanding the historical

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dynamics of differentiation and exchanges between populations that shaped the current distribution of Eurasian species and their future survival. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **107**, 611–623.

ADDITIONAL KEYWORDS: Anatolia – biogeography – Fourier analysis – genetic differentiation – geometric morphometrics – Gliridae – mitochondrial cytochrome *b* – molar shape – Thrace.

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INTRODUCTION

Environmental conditions largely control the distribution of species, either through the direct impact of abiotic parameters such as temperature or precipitation on metabolic properties, or by indirect effects on the ecology of the animals, including changes in their habitat. Hence, past environmental changes contributed to mould their current distribution and diversity. Focus is often put on the climatic oscillations associated with the Quaternary glacial/interglacial cycles. Their impact was particularly important on forest species, as glacial periods were associated with an extension of open landscape, leading to the retraction of forest environments and the associated fauna in geographically restricted areas, i.e. glacial refugia (e.g. Hewitt, 1996, 1999, 2000; Taberlet *et al*., 1998). More recent events associated with changes in forest distribution such as historic and even prehistoric phases of deforestation (Kaplan *et al*., 2011; Klein Goldewijk *et al*., 2011) might have impacted forest species as well. Studying the distribution of forest species might thus shed precious light on how forest dwellers faced perturbations of their environment at different time scales, providing relevant clues about the potential impact of the current global change on this kind of habitat, which is particularly prone to disturbance and fragmentation.

The edible dormouse (*Glis glis*) is a relevant model to tackle these questions, as this small mammal is strictly associated with the forest environment. Therefore, like the forests, it probably survived the Quaternary climatic cycles through important fluctuations in its distribution area, tracking changes in the range of the forests themselves. Its relatively sedentary habits (Hönel, 1991; Morris, 1997) and its marked preference for deciduous woodlands (Kryštufek, 2010) could also make it prone to suffer as a result of recent forest fragmentation.

The aim of the present study is therefore to investigate if and how the edible dormouse differentiated in structured populations according to changes in its forest habitat, with a focus on an understudied zone of its distribution, namely throughout its Turkish range. This area is of interest for biogeographical studies for several reasons. First, at the time scale of Quaternary climatic fluctuations, the importance of eastern refuge zones is increasingly being recognized (e.g. Michaux *et al*., 2004; Wielstra *et al*., 2010). The Balkanic refuge zone has recently been studied (Deffontaine *et al*., 2005; Macholán *et al*., 2007), but the role of possible refuge areas in the Near and Middle East region remains understudied due to a sampling bias in favour of European regions. Nevertheless, the Caucasus and its foothills close to the south-eastern coast of the Black Sea deserves additional interest as a possible refuge zone for Eurasian species (Santucci, Emerson & Hewitt, 1998; Seddon *et al*., 2002; Wielstra *et al*., 2010). In this context, biogeographical studies through Turkey are of key importance, because this area corresponds to a potential crossroads of populations expanding eastwards from European refuges and westward from Asian refuges. A second line of interest regarding this Turkish area is that today forest environments cover most of the Black Sea coast from the Marmara region to the foothills of the Caucasus, with subtle variations throughout this apparent continuous distribution. From west to east, climatic conditions grade from a Mediterranean to a more strongly seasonal Euro-Siberian climate (Güvenç, Öztürk & Oran, 2009). Anthropogenic deforestation and local variations in the precipitation regime (Sönmez *et al*., 2005) have caused local breaks in the forest, especially along the western Black Sea coast around Zonguldak (Fig. 1). This forest break is congruent with a break in the current distribution of the edible dormouse (Kryštufek, 2010; Fig. 1) suggesting that forest fragmentation might contribute to isolate populations of the species.

To investigate the population structure of the edible dormouse in this area of Turkey, two complementary approaches were combined. First, genetic analyses were performed to insert the variation of Turkish dormice within the known framework of European populations. Based on mitochondrial cytochrome *b* DNA, Europe as a whole appeared to be characterized by very low genetic diversity, with only a few endemic lineages occurring in the Italian peninsula (Hürner *et al*., 2010; Lo Brutto, Sara & Arculeo, 2011). The existence of a refuge zone in the foothills of Caucasus would be supported by evidence of a differentiated lineage in the eastern part of the Turkish range, a zone that was not thus far been documented. This genetic approach was completed by a study of the

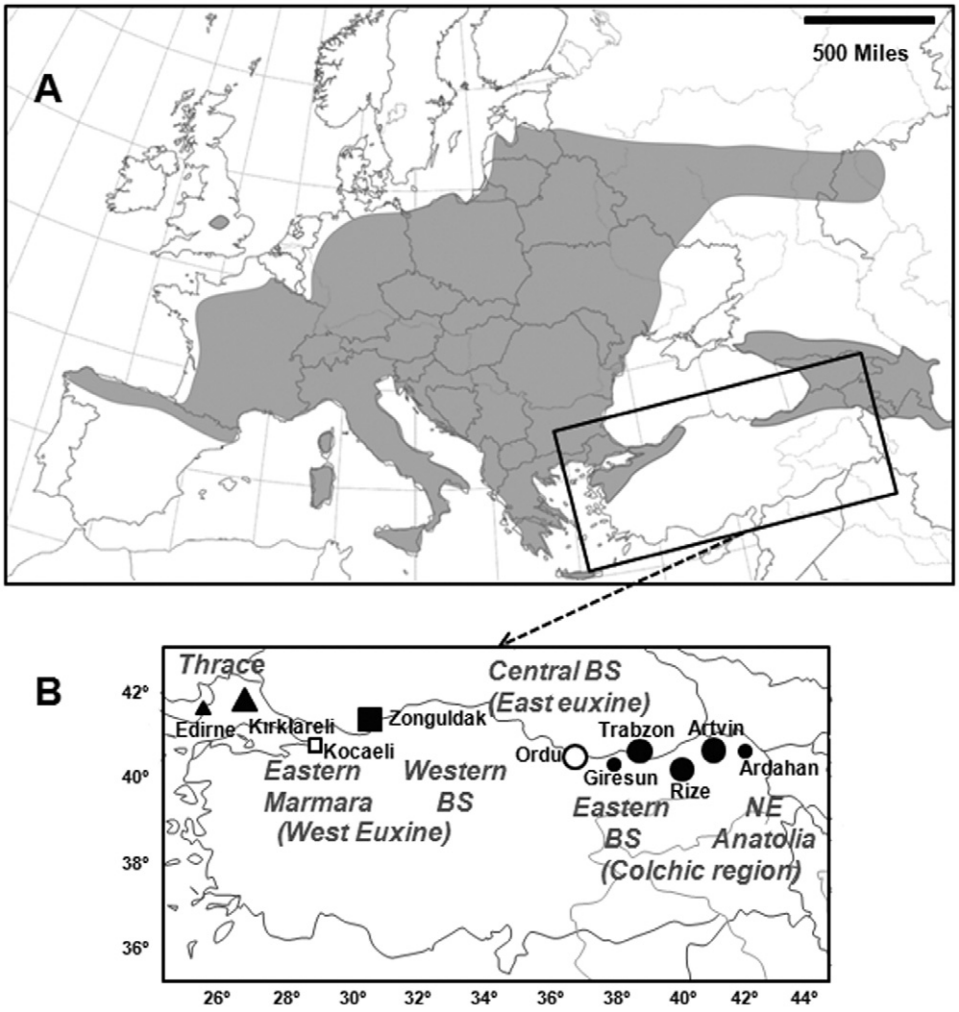


Figure 1. A, worldwide distribution of edible dormouse (*Glis glis*) (based on Hürner *et al*., 2010); B, enlargement showing the sampling area (black triangles = Thrace, white square = eastern Marmara, black square = western Black Sea, white circle = central Black Sea, black circles = eastern Black Sea and north-eastern Anatolia with their phytogeographical regions in parentheses; small symbols = localities documented by a single specimen).

phenotypic variation based on an extensive sampling throughout the Turkish range.

Morphological characters can be markers of intraspecific biogeographical structure, because they can diverge due to neutral genetic divergence among isolated lineages, and/or as an adaptive response to environmental conditions (Thorpe, 1987; Fadda & Corti, 2001; Cardini, 2003; Monteiro, Duarte & dos Reis, 2003; Renaud, Chevret & Michaux, 2007; Deffontaine *et al*., 2009; Ledevin *et al*., 2010). Among possible morphological features, teeth have been suggested to provide good markers of the population structure even over short time scales (Renaud, 2005; Renaud & Michaux, 2007) because they are not prone to plastic variations such as in bone features like mandibles (Renaud & Auffray, 2010). The first upper molar (UM1) was selected for morphometric studies because this tooth appeared to deliver valuable phyletic information in diverse glirids (e.g. Pavlinov, 2001) and many other rodents (e.g. Misonne, 1969; Michaux, 1971; Leamy & Sustarsic, 1978; Renaud, 2005; Renaud *et al*., 2005; Macholán, 2006). Its size and shape variations were quantified through a morphometric analysis of the tooth outline, a character and an approach that has been shown to be very efficient at describing subtle geographical variations in rodents (Renaud, 1999; Renaud & Michaux, 2007).

MATERIAL AND METHODS

Material

The present study is based on the collection of edible dormice (*Glis glis*) from the Laboratory for Systematic of Vertebrate Animals (Ankara University, Turkey).

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The animals were trapped between 1991 and 2008 in different localities from the Thrace, Marmara region and a broad longitudinal coverage along the Black Sea coast (Fig. 1B), using wooden live-traps or picked up directly from hollow trees. The sampling locations are scattered along a thin coastal strip roughly corresponding to the extension of the eco-region known as 'Euxine-Colchic' deciduous forest, ranging in Turkey from the south-eastern Bulgarian border to the west to Georgia to the east. Localities can be grouped into six geographical areas: (1) Thrace on the European continent, west of the Marmara Sea; (2) eastern Marmara region; (3) western Black Sea coast, ending to the east of Zonguldak; (4) central Black Sea region, up to the Melet River just eastward of Ordu; (5) the eastern Black Sea coast; and (6) north-east Anatolia, corresponding to inland locations close to the Caucasus foothills (Artvin, Ardahan).

These areas in turn correspond to three local eco-regions: (i) Thrace (1) and the neighbouring West Euxine region, including eastern Marmara (2) and western Black Sea coast (3), all corresponding to areas of dry Euxinic(-like) forests, tending to support a high diversity of tree species; (ii) East Euxine, roughly corresponding to the central Black Sea coast (4) and including slightly humid Euxine areas located west of the Melet river; and (iii) Colchic zone, including all eastern localities (5 and 6) and corresponding to humid areas with old-growth forest with low tree species diversity.

Genetic analyses were performed on 14 specimens from Kırklareli (Thrace: $N = 4$), Kocaeli (eastern Marmara: East Euxine zone, $N = 1$), Zonguldak (western Black Sea: West Euxine zone, $N = 2$), Ordu (central Black Sea, $N = 2$), Trabzon (eastern Black Sea: Colchic zone, $N = 1$), Rize (eastern Black Sea: Colchic zone, $N = 2$), and Artvin (eastern Black Sea: Colchic zone, $N = 1$). These specimens were compared with animals already analysed in previous studies (see Hürner *et al*., 2010) to check the genetic relationship between European and Turkish edible dormice populations. Sixteen mitochondrial cytochrome *b* (cyt-*b*) haplotype sequences were downloaded from the GenBank database and were used for the genetic analyses (accession numbers: FM160651–FM160665, FM160733, and FM160734). These haplotypes corresponded to 130 *G. glis* specimens from different European regions: Spain, France, Belgium, Italy, Sicily, Germany, Slovania, Russia, Great Britain, Switzerland, Macedonia, Montenegro, Czech Republic, Bosnia–Herzegovina, Croatia, and Lettony.

For morphometric analyses, skulls of the specimens were prepared as museum material. The UM1 of 51 specimens was measured (Table 1). All animals could be considered as adult based on the fact that all molars were erupted.

Table 1. Trapping localities with their attribution to a geographical group, latitude and longitude, and number of first upper molars (UM1) measured in the present study

Locality	Region	Latitude (°N)	Longitude (°E)	No. of UM1
Edirne	Thrace	41.40	26.34	1
Kırklareli	Thrace	41.44	27.15	16
Kocaeli	Eastern Marmara	40.45	29.50	1
Zonguldak	Western Black Sea	41.15	31.24	6
Ordu	Central Black Sea	40.55	37.53	6
Giresun	Central Black Sea	40.55	38.30	1
Trabzon	Eastern Black Sea	41.0	39.45	6
Rize	Eastern Black Sea	41.0	40.30	10
Artvin	Eastern Black Sea	41.14	41.44	3
Ardahan	Eastern Anatolia	41.11	42.41	1

METHODS

Genetic analyses

The mitochontrial cyt-*b* gene was amplified using specific primers designed for *Glis glis* (Hürner *et al*., 2010). MODELTEST 3.0 (Posada & Crandall, 1998) was used to determine the most suitable model of DNA substitution for the cyt-*b* data set studied. Phylogenetic reconstructions were performed using the maximum-likelihood criterion (ML; Felsenstein, 1981) implemented in PHYML (Guindon & Gascuel, 2003). Phylogenetic trees were rooted with cyt-*b* sequences from one specimen of the garden dormouse (*Eliomys quercinus*) and one specimen of the hazel dormouse (*Muscardinus avellanarius*) as suggested by Hürner *et al*. (2010). The robustness of the tree was assessed based on bootstrap support (BS) (1000 random pseudoreplicates).

Morphometric analysis

Outline analysis

The occlusal surface of each dental row was placed parallel to the focal plane and digital images were taken using a Leica MZ 16 stereomicroscope equipped with a Leica DFC 320 camera. The two-dimensional outline of the tooth was digitized on the left upper molar row or from a mirror image of the right molar when the left one was missing or damaged. The starting point of the outline was defined at the contact point between the UM1 and the premolar (Fig. 2).

For each molar, 64 points at equally spaced intervals along the outline were sampled using the Optimas software (version 6.5). This set of *x*,*y*-coordinates was then analysed using an elliptical Fourier analysis (EFA) using the software EFAwin (Ferson, Rohlf & Koehn, 1985). This method is based on separate Fourier decompositions of the incremental changes along *x* and *y* as a function of the cumulative length along the outline (Kuhl & Giardina,

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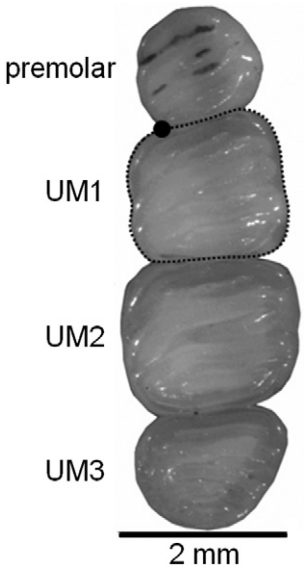


Figure 2. Upper molar row of edible dormouse in occlusal view. The studied outline is superimposed on the first upper molar (UM1), with the starting point (black dot) at the meeting point between the premolar and the UM1. Lingual side to the left, anterior part to the top.

1982). The outline is approximated by a sum of trigonometric functions of decreasing wavelength: the harmonics. Each harmonic is then defined by four coefficients: A_n and B_n for x, and C_n and D_n for y, defining an ellipse in the x–y plane.

The first harmonic corresponds to the best-fitting ellipse to the outline. Its major axis was taken as the new x-axis to adjust the orientation of the outline (Rohlf, 1990). Its area was used to standardize the Fourier coefficients (FCs) for size differences to eliminate isometric size effects and to concentrate on shape information only.

As the coefficients A_1, B_1, and C_1 correspond to residuals after standardization (Crampton, 1995; Renaud *et al*., 1996) they were not included in the subsequent statistical analysis. The coefficient D_1 still retains information about the elongation of the outline (Michaux, Chevret & Renaud, 2007). It was thus included in the statistical analyses.

Using a Fourier analysis, the higher the rank of the harmonic, the more detailed is the description of the outline. The number of harmonics selected for subsequent statistical analyses should take into account the level of measurement error occurring during data acquisition and the information content of each harmonic. To evaluate the adequate threshold harmonic for analysis of dormouse teeth, the shape of one UM1 was measured ten times, providing an estimate of the measurement error for each harmonic (Fig. 3). Measurement error was estimated as the percentage of error for the amplitude of each harmonic (square root of the sum of the squared FCs A_n, B_n, C_n, and D_n). In the case of a dormouse tooth, measurement error was low (< 5%) until the fifth harmonic and abruptly increased thereafter (Fig. 3).

The information content of each harmonic was estimated as follows. The amplitudes of the harmonics were cumulated over the total range of harmonics, and the information brought by each harmonic was then estimated as the percentage of this sum represented by this harmonic (Crampton, 1995). Each of the five first harmonics significantly increased the amount of shape information up to 97% of the total information (Fig. 3). A plateau was then reached, showing that the subsequent harmonics provided almost no further relevant shape information.

Hence, the set of the first five harmonics appeared to provide a good compromise between measurement error, information content, and the number of variables to be considered. A data set of 17 variables (20 FCs minus A_1, B_1, and C_1) was thus retained for subsequent analyses.

A visualization of shape differences between UM1 was provided by the reconstruction of outlines using the inverse Fourier method (Rohlf & Archie, 1984).

Statistical analyses

The size of UM1 was estimated from the square root of its two-dimensional outline area to avoid a magnification of any size difference due to quadratic effects, an area being of squared linear dimension. Differences between regions or between localities were tested using analyses of variance (ANOVA) completed with a non-parametric test (Kruskal–Wallis). A possible relationship with longitude was investigated using a linear regression.

Multivariate analyses were used to investigate patterns of shape differences. Multivariate analyses of variance (MANOVA, test considered: Wilks' lambda) were performed on the set of 17 FCs to test for differences between the end-members of the Turkish distribution (Thrace vs. East Euxine and Colchic regions). These geographical end-members were used as the reference data set to investigate the affinities of the West Euxine specimens as well as single specimens from four localities (Edirne, Kocaeli, Giresun, and Ardahan).

A canonical analysis was uses to further investigate the relationships between localities to address the patterns of geographical differentiation independently of any a priori definitions of geographical zones. This analysis provided canonical shape axes on which patterns of among-group differentiation were represented. Localities sampled by a single specimen (Edirne, Kocaeli, Giresun, and Ardahan) were not included in the computation but added as supplementary specimens.

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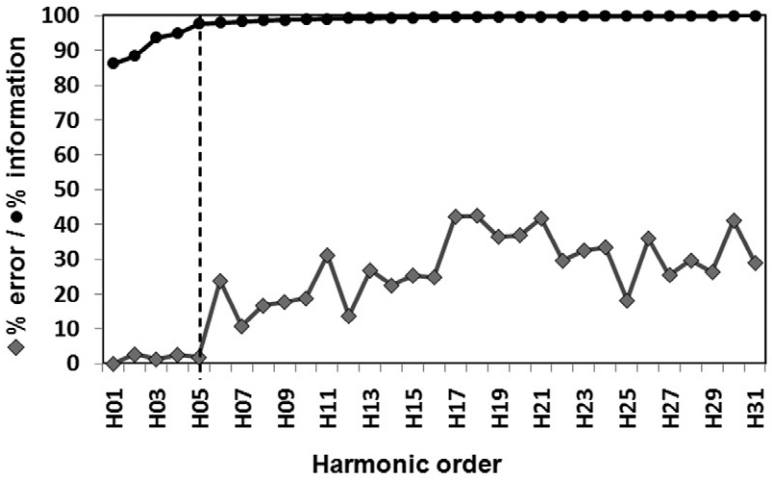


Figure 3. Measurement error (grey diamonds) and cumulative power (black dots) as a function of the harmonic order for the elliptic Fourier transform of the edible dormouse first upper molar outline. The measurement error is expressed as the coefficient of variation of the harmonic amplitude (= square root of the sum of the squared Fourier coefficients) of one specimen measured ten times. The cumulative power corresponds to the contribution of each harmonic (%) to the total information (i.e. the sum of all harmonic amplitudes = 100%).

All statistical analyses were performed using SYSTAT (Version 11, Systat Software Inc., Richmond, CA, USA) software programs.

Shape changes along the canonical axes were visualized using outlines obtained by an inverse Fourier method. For this purpose, FCs corresponding to extreme scores along the axes were calculated using a multivariate regression of the FCs upon the relevant canonical axis (Monti, Baylac & Lalanne-Cassou, 2001). This procedure, as well as the inverse Fourier analysis, was performed using NTSYSpc 2.2 (Rohlf, 2004).

RESULTS

Mitochondrial DNA analyses

Sixteen haplotypes were identified among the 143 *G. glis* specimens examined. The matrix included 831 bp for each specimen, of which 72 sites were variable and 19 were parsimony-informative. The average transition–transversion ratio was 3.9, and nucleotide frequencies were 31.9, 27.1, 28.4, and 12.6% for T, C, A, and G, respectively. ML analyses were performed using the GTR + Gamma model suggested for the data by the Akaike information criterion in MODELTEST, with the proportion of invariable sites equal to 5.361 and the gamma distribution shape parameter equal to 0.33. The ML phylogenetic tree (Fig. 4) showed that the 16 *G. glis* haplotypes fell into three major lineages: the first comprised some individuals from Sicily and one from Calabria (Aspromonte, Italy) (Lineage 1; ML BS = 77%); the second lineage corresponded to populations from southern Italy, including a few Sicilian specimens (Lineage 2; BS = 90%); and the third lineage comprised populations from northern Italy, western, central and eastern Europe, as well as all the Turkish specimens (Lineage 3; BS = 90%). Note that all Turkish specimens are characterized by a single haplotype, corresponding to haplotype 2 of Hürner *et al*. (2010), which is further distributed throughout Europe. Genetic divergence among these three lineages was low, varying from 0.5 to 1.5% Kimura 2-Parameter (K2P) distance (Kimura, 1980).

Variation in molar size

The size of the first upper molar varied across the geographical range documented in the present study, with largest teeth to the west and smallest teeth to the east (Fig. 5). Hence, the Thrace molars appeared significantly larger than the East Euxine and Colchic teeth (ANOVA and Kruskal–Wallis: $P < 0.001$), but this could also correspond to a gradual decrease in size with teeth from the West Euxine being intermediate in size, belonging to the range of variation of both the Thrace and the north-eastern Turkish localities (Fig. 5). Accordingly, tooth size and longitude were significantly related (linear regression: $R^2 = 0.561$, $P < 0.001$). This relationship held true even when focusing on north-eastern Turkey only ($R^2 = 0.401$, $P = 0.001$). A clear-cut boundary between groups was thus not visible across our geographical distribution.

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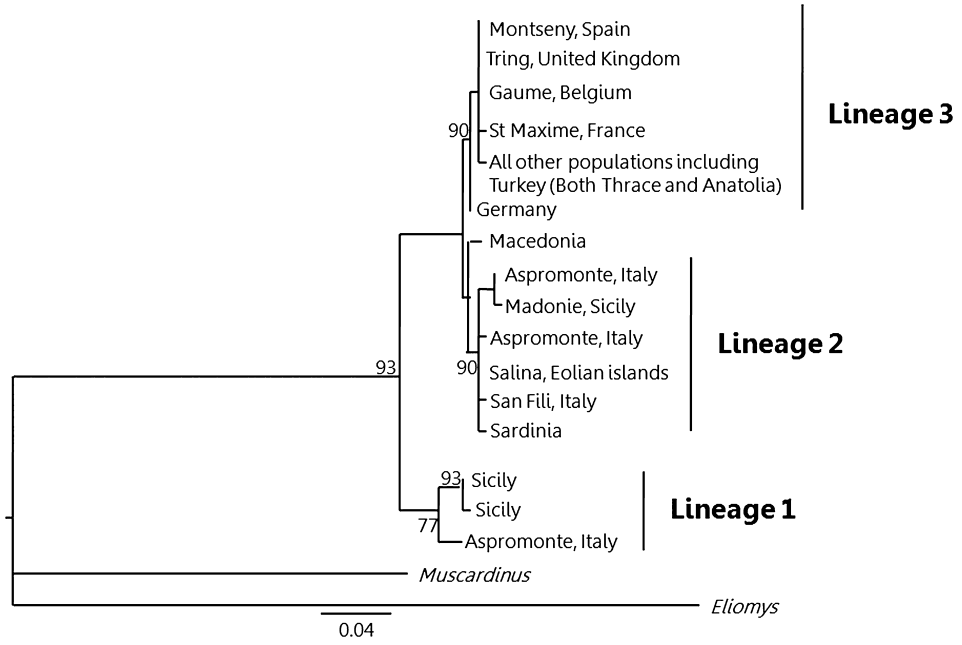


Figure 4. Maximum-likelihood tree for the 16 haplotypes identified in edible dormouse (*Glis glis*). Localities where the haplotypes were found are given on the right of the tree. Numbers at nodes indicate maximum-likelihood bootstrap values greater than 50%. Maximum likelihood distance for the scale bar.

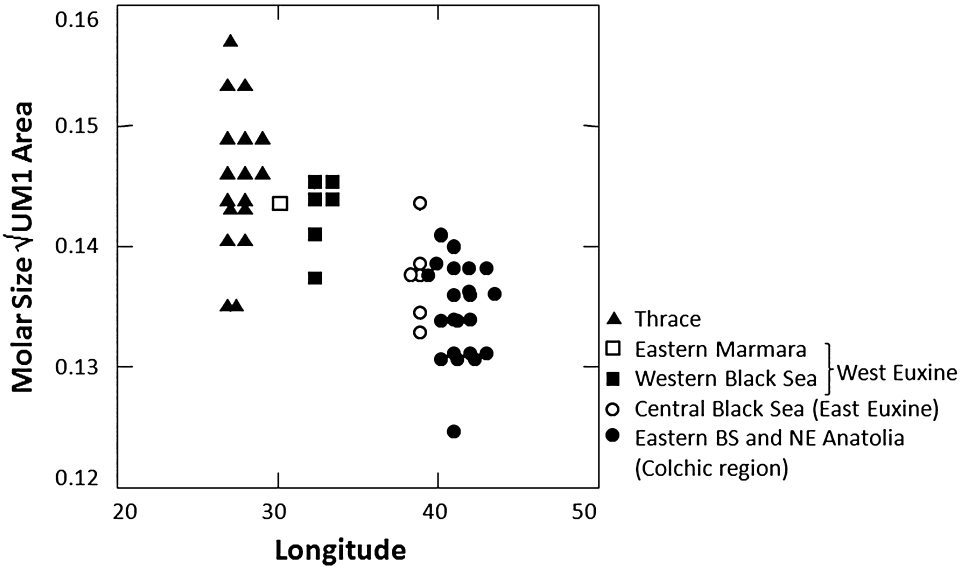


Figure 5. Distribution of the first upper molar (UM1) size, estimated by the square root of the tooth outline area, of dormice in the different localities along the northern part of Turkey, plotted as a function of longitude. Each dot represents one tooth.

Molar shape differentiation along the Black Sea coast

The two groups constituted by dormice from Thrace vs. north-eastern Turkey (East Euxine and Colchic regions) differed significantly in molar shape (MANOVA: $P = 0.0040$). This differentiation between the two groups led to a good percentage (> 80%) of reclassification of the original groups (Table 2), although jack-knifed reclassification was not as good and suggested an overlap between the two groups. An inverse elliptic Fourier transform allowed us to visualize differences in UM1 shape between the two groups. Thrace teeth were more diamond- to oval-

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Table 2. Differentiation between dormice from north-western vs. north-eastern Turkey (Trabzon, Rize, Artvin, and Ardahan) based on the shape of their first upper molars

	NE Turkey (East Euxine and Colchic region)	NW Turkey (Thrace)	Correct reclassification
Anatolia	22	3	88% (76%)
Thrace	0	16	100% (75%)
Zonguldak	4	2	
Edirne		1	
Kocaeli		1	
Giresun	1		
Ardahan	1		

Specimens from Zonguldak and single specimens from Edirne, Kocaeli, Giresun, and Ardahan were added as supplementary specimens and classified a posteriori to the reference groups. Percentages of reclassification are given, with the percentage of reclassification after a jackknifed procedure in parentheses.

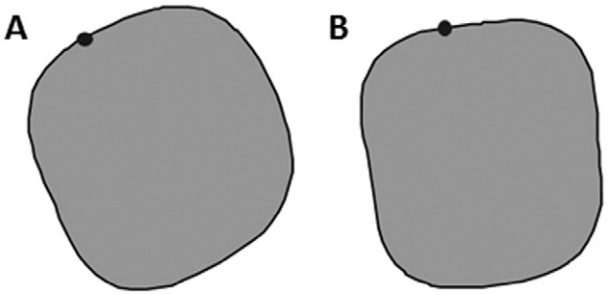


Figure 6. Reconstructed outlines exemplifying the shape difference between first upper molars from (A) Thrace and (B) north-eastern Turkey. Outlines correspond to the average values for each group, based on the coefficients of the first five harmonics of the elliptic Fourier transform. Anterior part to the top, lingual side to the left. The oval shape of Thrace molars, compared with the square shape of teeth from north-eastern Turkey, influences the orientation of the outline according to the first ellipse and contributes to the different orientation between the two reconstructed outlines.

shaped (Fig. 6A) whereas north-eastern Turkey specimens tended to display a square-like molar shape (Fig. 6B).

Specimens from the western Black Sea coast (Zonguldak district) were attributed to both Thrace and north-eastern Turkish morphologies. This suggested that this region was a contact area where specimens from the eastern and western populations would co-occur (Table 2).

Interestingly, attributions of single specimens from Thrace and the Colchic region were in full agreement with their geographical location (Table 2). The specimen from Kocaeli, located on the eastern Marmara coast, appeared to be associated with Thrace dormice on the basis of its molar shape.

These results supported the existence of two differentiated groups of edible dormice, roughly corresponding to European vs. easternmost regions of Turkey with a zone of overlap along the western Black Sea coast. The attribution of the Kocaeli specimen to the Thrace group, together with the mixed composition observed in Zonguldak, did not support the hypothesis of a boundary corresponding to the Marmara straits and rather supported a differentiation corresponding to the two parts of the distribution area of the edible dormouse (see Fig. 1B).

To further investigate the pattern of shape differentiation, a second canonical analysis was performed using the localities as groups. Again, significant geographical differentiation was apparent ($P < 0.0001$).

The first axis (CA1, 52.5% of the among-group variance) mainly represented the differentiation between the east and west populations, confirming the important geographical differentiation in molar shape between Thrace and north-eastern Turkey (Fig. 7). Again, however, the sample from the eastern Marmara region (Kocaeli) was clearly associated with Thrace, whereas Zonguldak (western Black Sea) was associated with the eastern Black Sea coast. A secondary differentiation seemed to occur within the eastern region, with the central Black Sea coast (Ordu) separated from the Colchic localities (Trabzon, Rize, Artvin, and Ardahan) along the second axis (20.3%). Reconstructed outlines visualizing extreme scores along the axis showed that this differentiation involves subtle shape changes. Molars from the central Black Sea coast tended to have straight zones of contact with the premolar and the second molar, whereas teeth from the Colchic area were more rounded in these areas.

Of note, the single specimens added as supplementary individuals in the analysis were plotted according to their geographical location (Edirne with Thrace, Ardahan with Colchic localities, and Giresun intermediate between the central and eastern Black Sea coast).

DISCUSSION

Genetic homogeneity vs. morphometric east–west differentiation: what evolutionary scenario?

The present study constitutes a first attempt to quantify the geographical variation of the edible dormouse

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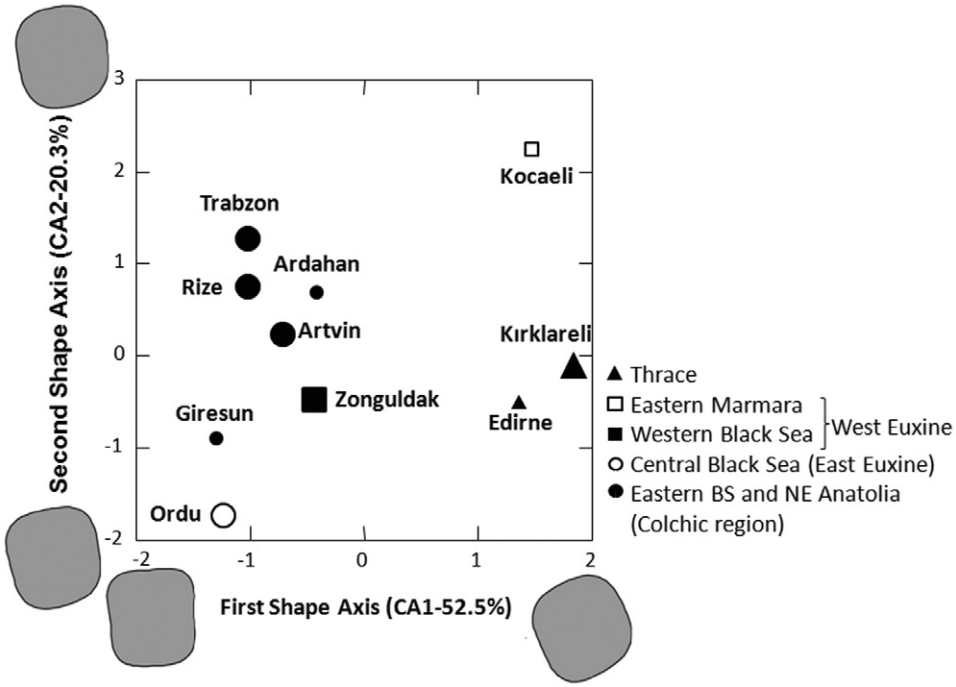


Figure 7. Shape variation of the first upper molar (UM1) within the edible dormouse in Turkey, displayed on the first two axes of a canonical analysis on the Fourier coefficients. The grouping variable corresponds to the localities of trapping. Each symbol corresponds to the mean of one locality. Single specimens are indicated by small symbols. Reconstructed outlines show the shape changes along the canonical axes. They correspond to extreme scores (CA1 = ±2 and CA2 = ±2).

in an underdocumented zone of its distribution area, namely the northern part of Turkey, which may be of considerable biogeographical importance in documenting the contact between European and Asiatic populations of Eurasian species. In this regard, conflicting evidence was provided by genetic and morphometric analyses. Molar size and shape suggested a complex geographical structure of the Turkish dormice populations, with a primary differentiation opposing European (Thrace) and north-eastern Turkey (Colchic region) populations, in agreement with recent genetic analyses based on fast evolving markers of intra-specific differentiation [random amplification of polymorphic DNAs (RAPDs), Selçuk *et al*., 2012]. In contrast, analysis of the mitochondrial cyt-*b* gene revealed a surprising homogeneity not only within the Turkish range of the edible dormouse, but also of the Turkish dormice when compared with the whole of Europe.

The strong east–west morphological differentiation suggested at first glance an ancient separation between the populations, allowing the accumulation of significant phenotypic differences as the passive consequence of isolation. A long-term isolation between Asian and European populations during the successive glacial–interglacial cycles appeared to be a plausible hypothesis. The eastern Black Sea coast towards the foothills of the Caucasus increasingly seems a possible refuge zone for European species (Santucci *et al*., 1998; Seddon *et al*., 2002; Wielstra *et al*., 2010). Indeed, it seems likely that forest habitats persisted there during glacial phases (Svenning, Normand & Kageyama, 2008; Tarkhnishvili, Gavashelishvili & Mumladze, 2012), including tree species such as the sweet chestnut (*Castanea sativa*) (Krebs *et al*., 2004) on which the edible dormouse heavily relies for food and shelter, making the zone a possible glacial refuge for this species.

This interpretation is, however, undermined by the genetic homogeneity observed throughout the European and Turkish range of the edible dormouse based on the mitochondrial cyt-*b* gene, and interpreted as a result of a post-glacial expansion from a single refuge probably located in the Italian peninsula (Hürner *et al*., 2010). This suggests that despite the apparently high chance of survival in other refuges (Iberic peninsula, Balkan, as well as eastern Black Sea coast), the edible dormouse went extinct there during the glacial maxima, possibly due to its overall low abundance making the risk of random extinction quite high. The existence of adequate habitats would have allowed a fast post-glacial recolonization, as evidenced by the reappearance of the dormouse in the fossil record soon after the end of the last glacial

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maximum (e.g. Cuenca-Bescós *et al*., 2009). Yet, this interpretation also means that the phenotypic and RAPDs genetic differentiation took place in an evolutionary quite short time span of less than around 10 000 years.

A complex boundary between European and Asian populations

For many European species, including the edible dormouse, Turkey appears at the crossroads of populations from western and eastern areas. Yet, depending on the species, the location of the area where eastern and western lineages meet varies, either corresponding to the Marmara straits or eastwards along the Black Sea coast. A range of species document each of the cases: European and Asiatic lineages meet at the Marmara straits in hedgehogs (Seddon *et al*., 2002) and yellow-necked field mice (Michaux *et al*., 2004) but slightly eastwards for newts (Wielstra *et al*., 2010), turtles (Fritz *et al*., 2008), free-living mice (Macholán *et al*., 2007), and wood mice (Michaux *et al*., 2003). Regarding the edible dormouse, the first description of a differentiation between European and Asiatic groups, identified as subspecies (*G. glis pindicus* in Thrace and *G. g. orientalis* in Anatolia) proposed a boundary corresponding to the Marmara straits (Doğramacı & Tez, 1991). Yet, that study included no sample between the Marmara strait and the region of Zonguldak, hindering a precise location of the boundary between the two groups. The present results, in contrast, suggest that the boundary between European and Asiatic dormice is located eastwards of the Marmara straits, and probably corresponds to the recorded break in the distribution area of the edible dormouse (Kryštufek & Vohralík, 2005). Again, morphometric results are in agreement with genetic data based on fast evolving markers, clustering Zonguldak with Thrace (Selçuk *et al*., 2012).

The various locations of the contact zone between European and Asiatic lineages depending on the species considered point to the complexity of the factors involved. The Marmara strait, as a water mass, constitutes an intuitive geographical barrier for terrestrial species. Yet, being shallow, it became dry during most glacial periods and hence did not constitute a permanent barrier (Demirsoy, 2008). Furthermore, its limited width might allow easy crossing by a species with good swimming ability such as the edible dormouse (Kryštufek, 2010).

Other factors thus need to be invoked to explain a contact zone located eastward of the Marmara strait, along the north-western coast of the Black Sea. Climatic variations might be involved, as this region corresponds to the transition between a Mediterranean-like and a Euro-Siberian climate (Güvenç *et al*., 2009), with a dry segment between Zonguldak and Ordu where forest vegetation is scarce (Tarkhnishvili *et al*., 2012). Apart from a possible impact on the ecology and thermoregulation of the edible dormouse, this climatic transition impacts the vegetation (e.g. Fang & Lechowicz, 2006). This vegetational factor may be crucial for an animal that is highly dependent for food and shelter on mature deciduous woodland with mast seeding trees, particularly beeches (*Fagus* sp.), oaks (*Quercus* sp.), and the sweet chestnut. Isolation between edible dormouse populations may have been further promoted by anthropogenic deforestation, increasing in Anatolia over historical times (e.g. Mayer & Aksoy, 1986; Atalay, 1992; Çolak & Rotherham, 2006).

These hypotheses are not mutually exclusive and point to the fact that focusing on putative precise geographical barriers such as the Marmara straits may be a simplification of a more subtle reality integrating diverse aspects of the animal's ecology.

Complex ecological control for a step-wise differentiation along the Black Sea coast?

Beyond the main differentiation between European and Asian dormice, our results evidenced a further geographical differentiation along the Black Sea coast, separating dormice from the central Black Sea coast (Ordu) from those located eastwards (Trabzon, Rize, Artvin, Ardahan), in agreement with the differentiation observed based on fast evolving genetic markers (Selçuk *et al*., 2012). This differentiation corresponds to a rather progressive change in tooth size and a step-wise differentiation for tooth shape; it is not reflected in the differentiation of the mitochondrial cyt-*b* gene, suggesting a three-fold process leading to the present pattern of differentiation: (1) post-glacial recolonization from a single refuge, explaining the homogeneity of the cyt-*b* gene; (2) isolation of west and east populations; (3) further isolation of East Euxine vs. Colchic populations. Factors driving this differentiation might again mix ecological, vegetational, and climatic aspects. From the west to the east of the Black Sea coast, the Euro-Siberian climate gradually increases in seasonality (Akman, 1995, 2011), a factor that may explain the gradual change in tooth size of the edible dormouse and favour a differentiation in tooth shape. Furthermore, a fragmentation in the distribution of beeches and chestnuts is recorded between the Ordu and Trabzon regions (Eşen, 2000; Maurer & Fernández-López, 2001; Aydınözü, 2008) that may be due to a combination of anthropogenic fragmentation, climatic, and topographic factors. All these factors may contribute to hinder gene flow from east to west for dormice just as for trees.

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Of note, the two areas where a differentiation occurred (western Black Sea coast around Zonguldak and transition between Euxine and Colchic regions around Giresun) both correspond to areas where risks of drought increase even close to the Black Sea coast (Sönmez *et al*., 2005). Drought years in forest environments are likely to negatively impact mast production (Pérez-Ramos *et al*., 2010). Periods of food shortage may lead edible dormice to postpone reproduction (Schlund, Scharfe & Ganzhorn, 2002; Bieber & Ruf, 2009). Areas of higher drought vulnerability might thus be unfavourable to persistent dormice populations despite apparently favourable conditions.

In conclusion, a combination of ecological and climatic factors probably reduced gene flow between populations after recolonization from a single refuge. This recent fragmentation triggered the accumulation of neutral genetic divergence (Selçuk *et al*., 2012) and concomitant phenotypic differentiation. However, we still lack data to further interpret this morphological differentiation in tooth size and shape: it could have accumulated by neutral genetic divergence; and an adaptive component to the different environments might have further accelerated morphological evolution (Renaud *et al*., 2007) especially as reduced gene flow may help populations to track their local adaptive optimum (Lenormand, 2002).

Such an intricate interplay of ecological factors might also have contributed to the extinction of the edible dormouse in apparently suitable refuge areas during glacial periods. It might also represent a current underestimated threat to this rare species as global climate change is increasing drought in Mediterranean regions, thus impacting forest trees and the associated fauna.

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