



More Insights into the Evolution of Fat Dormouse in the Old Growth Hyrcanian Forests

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ABSTRACT

Fat dormouse (*Glis glis*), belonging to the monotypic genus *Glis* of the family Gliridae, has been frequently used as a model to enrich our knowledge of patterns of arboreal species adaptation to the glacial oscillations. Ancient Hyrcanian forests, as one of the old-growth relicts of the temperate deciduous forests, have been recently documented as an important refugium during the last glacial maximum (LGM). More investigations based on skull and mandible morphological assessments revealed considerable intraspecific evolutionary divergence among the local populations settled in the Hyrcanian forests of northern Iran. Geometric morphometric approaches in this study confirm the presence of multiple cryptic refugia for Fat dormouse as a small forest-dwelling species during paleontological oscillations. Such findings correspond to those of previous molecular and niche analyses. Our research also confirms an ideal capability of morphological approaches in species evolutionary assessments.

Article Information

Received 11 June 2018

Revised 30 August 2018

Accepted 31 January 2019

Available online 06 November 2019

Authors' Contribution

ZE, MK and MN performed statistical analysis and wrote the manuscript. MN prepared the samples. HRR helped in writing the manuscript while NK edited the manuscript.

Key words

Evolutionary divergence, *Glis glis*, Hyrcanian forests, Iran, Micro-refugia, Geometric morphometric.

INTRODUCTION

Ecological differences, macro-habitat features and different feeding habits can result in intraspecific morphological variations and subsequently molecular divergence (Richman and Price, 1992; Price *et al.*, 2014). Ecological variations along with changes in macro-habitat features generally cause predictable intraspecific distinction of the morphological characteristics (Richman and Price, 1992). Adaptation to the different eco-geographic conditions may result in the divergence of phenotypes, creation of different lineages, and possibly contribution to speciation (Naderi *et al.*, 2013). Combining molecular markers with phenotypic variation in phylogeographical investigations can help better understand the evolutionary mechanisms that may have an influence on species (Michaux *et al.*, 2007). Rodents are one of the most investigated mammalian groups known for rapid morphological adaptations in response to a number of potential factors driving such variations such as climate change (Gienapp, 2008; Pergams and Lawler, 2009) and

variation of growing season length (Ward *et al.*, 2000). However, it is not simply possible to relate the morphological attributes directly to the evolution without considering genetic properties as much of phenotypic plasticity can arise out of natural selection (Agrawal, 2001).

As an arboreal species tied completely to the deciduous Hyrcanian forests, Fat dormouse can be regarded as an ideal candidate to consider its morphological evolution in a phylogeographical context. More investigations on this species along the Hyrcanian refugium (Naderi *et al.*, 2013; Ahmadi *et al.*, 2018) revealed that the evolutionary variation of the Fat dormouse is directly related to its habitat features, particularly the climatic regime. Fat dormouse has been recently recognized as a polytypic species containing one completely distinct lineage in the most eastern parts of the Hyrcanian forests (Ahmadi *et al.*, 2018). It should be noted that based on mitochondrial evidences, the Iranian populations of the species have been recently introduced as a new and completely diverged lineage constituting more than 12 percent of intraspecific variation (Naderi *et al.*, 2013). Therefore, we aim to address the following questions: (i) is it possible to find such a deep morphological divergence that corresponds with genetic isolation? (ii) can morphology be able to distinguish among previously introduced genetic lineages? (iii) do

* Corresponding author: ghnadery@yahoo.com
0030-9923/2020/0001-0337 \$ 9.00/0
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morphological evidences support the molecular findings? (iv) with respect to the crucial role of the Hyrcanian forests as a major biodiversity hotspot in northern Iran (Naderi *et al.*, 2014), are there any intra-lineage differences within the populations belonging to the Iranian lineage?

In this study, we aimed (i) to quantify and compare the variation in skull morphology of *Glis glis* lineages known from different parts of its distributional range and (ii) to examine morphological variations of the populations distributed along the Hyrcanian forests of northern Iran (Iranian lineage). To investigate patterns of such potential intraspecific morphological divergence among lineages and sublineages (or populations), we applied geometric morphometric methods (Rohlf and Marcus, 1993; Zelditch *et al.*, 2004; Slice, 2007). These methods have been increasingly utilized to investigate morphological variation as well as adaptive radiation, particularly when studying features such as skulls and mandibles (Degrange and Picasso, 2010; Klingenberg and Marugan-Lobon, 2013). After analyzing morphological distances among lineages and populations, it will be possible to investigate factors potentially affecting morphological variation.

MATERIAL AND METHODS

Study area

The Hyrcanian forests of northern Iran cover an area of 1.8 million ha along the Alborz mountainous ridge (Forest, Ranges and Watershed Management Organization of Iran, 1386). These forests stretch from Astara in the west to Golidagh in the east in about 800 km length and a width of approximately 20 to 70 km. The Hyrcanian relict forests of northern Iran start from lower than sea level to an altitude of about 2800 meters above sea level and often consist of mixed types of Beech, Hornbeam, Oak, Maple, and Alder. More than 3234 vascular plant species have been reported from this area which can be classified into different forest zones such as sand dune vegetation, C4 dominated grass communities, aquatic plants, riverine and valley forests, alluvial, lowland, submontane, montane and subalpine deciduous forests, and so on (Akhani *et al.*, 2010). The distributional range of Fat dormouse (*Glis glis*) is within broad-leaved forest areas of Europe and South West Asia. The geographic range of the species distribution mainly matches the Palearctic deciduous

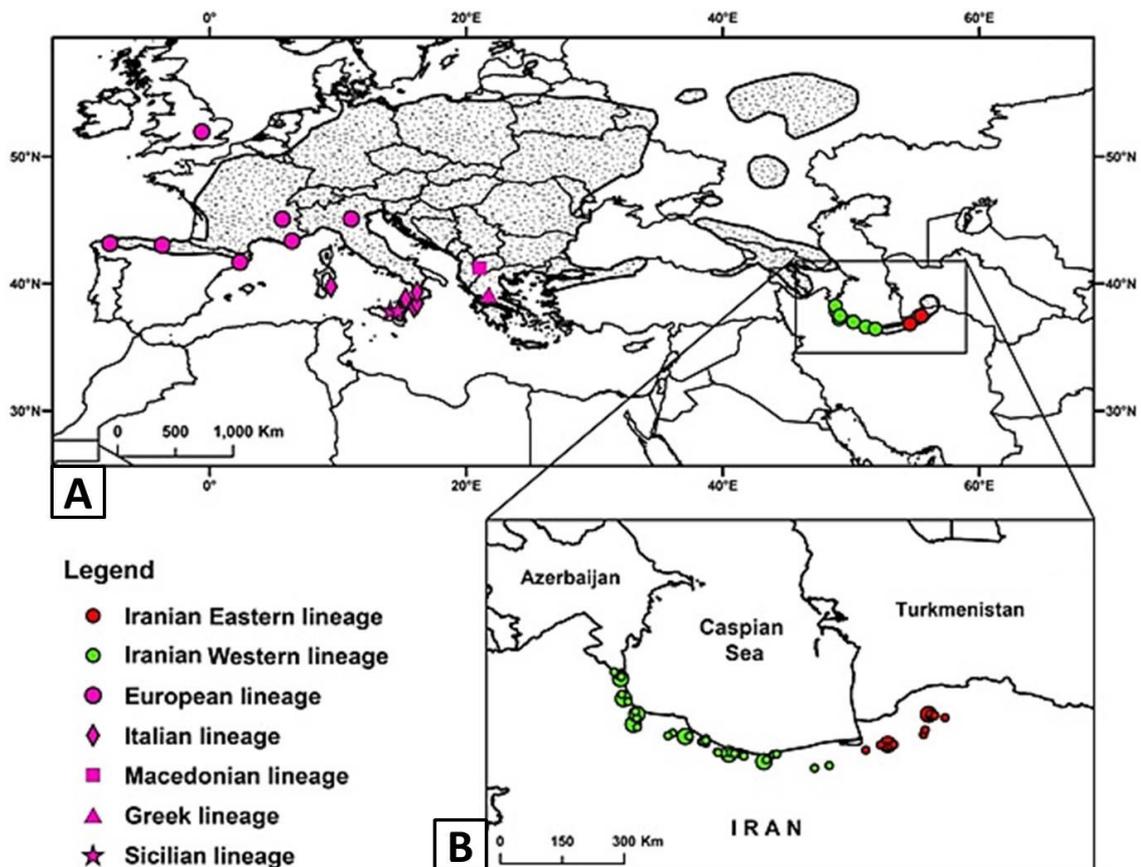


Fig. 1. Distribution of the studied species in the world (Naderi, 2014).

forest. The species is distributed from northern Spain through Central and South East Europe, the Atlantic coast, France and the major parts of the Iberian Peninsula (Krystufek, 2010). In the Caucasus region, the distribution extends to the southern coast of the Caspian Sea in Iran and to more remote areas such as the easternmost parts of Golestan province (Naderi *et al.*, 2013). A recent study also showed that the populations located in the easternmost part of the Hyrcanian forests of northern Iran have created a quite distinct lineage from western populations (Naderi, 2014). Figures 1 and 2 show the distribution of the known lineages and the phylogenetic relationships based on previous studies (Naderi, 2014).

Data collection and analysis

All specimens belonging to the Hyrcanian forests of northern Iran were photographed from specimens deposited in Arak University, biodiversity laboratory, while other specimens were photographed in the natural history museums located in St. Petersburg, Ljubljana, Moscow and Bonn. Based on previous studies (Hurner *et al.*, 2010; Naderi *et al.*, 2013) and later some initial cluster analyses,

we grouped specimens into six groups including European (including Europe and Turkey), Macedonian, Serbian, Caucasian, Russian (Krasnodar), and Iranian (Hyrcanian Eastern (hereafter Kalaleh), central and western parts (such as Heiran population)). The easternmost population in the Hyrcanian forests northern Iran was recorded in Kalaleh region. For all groups we verified size and shape of skulls from three views: lateral, ventral and abdominal. The number of specimens from each locality has been presented in Table I.

Table I.- The number of samples based on the locality and skull anatomical views.

	Lateral	Ventral	Dorsal
Europe	24	24	24
Caucasus	10	8	10
Krasnodar	19	19	20
Macedonia	22	23	22
Serbia	20	20	19
Iran (all of samples)	66	57	103

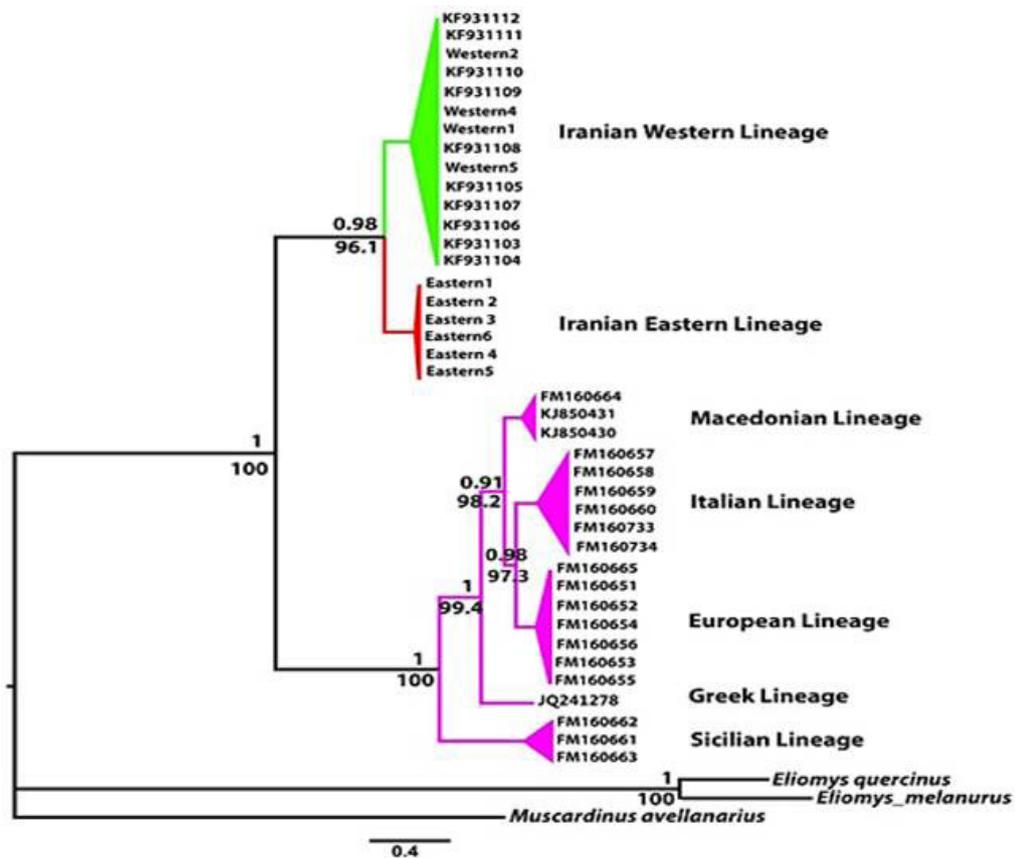


Fig. 2. Phylogenetic position of Iranian lineages based on mitochondrial evidences (Naderi, 2014).

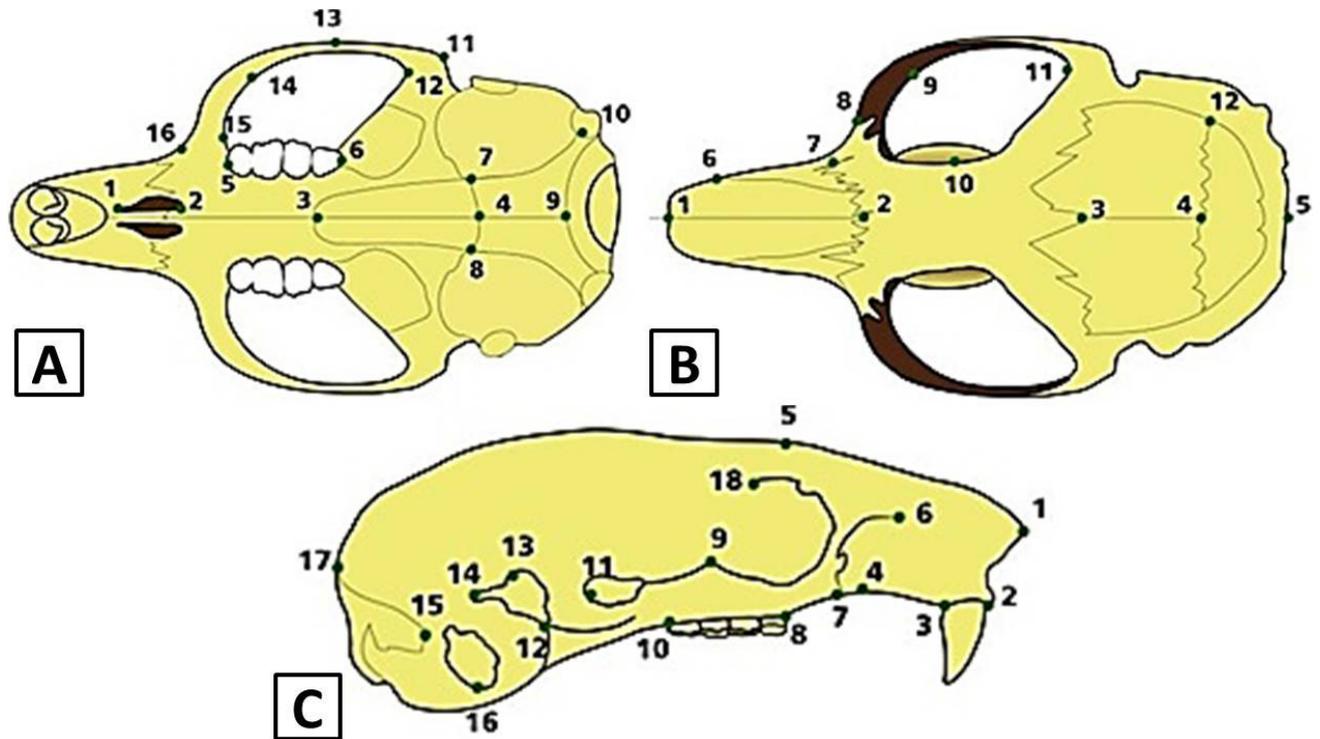


Fig. 3. Landmark positions on ventral (A), dorsal (B) and lateral (C) cranium views. **A**, Dorsal view: 1, frontal tip of internasal suture; 2, sagittal suture between frontals and nasals; 3, sagittal suture between frontals and parietals; 4, suture interception of both right and left parietal and interparietal in the sagittal plane; 5, posterior border of supraoccipital, at the nuchal crest; 6, anteriormost point of suture between nasal and premaxilla; 7, more concave curve point of zygomatic notch; 8, external border of maxillary at the most anterior curvature of zygomatic arch; 9, midpoint of the the zygomatic arch; 10, smaller frontal width (interorbital width); 11, more concave curve point of squamosal root of zygomatic arch; 12, suture between parietal, interparietal and occipital. **B**, Lateral view: 1, anterior tip of the nasals; 2, skull most posterior border, at supraoccipital bone, above the foramen magnum; 3, labial upper junction of incisors and maxillary; 4, lingual upper junction of incisors and maxillary; 5, posteriormost point of suture between nasal and premaxilla; 6, anterior border of zygomatic plate; 7, inferiormost point of suture between of premaxilla and maxilla; 8, anterior border of upper molar row at the alveolar process of maxillary; 9, internal more concave curve point of squamosal root of zygomatic arch; 10, posterior border of upper molar row at maxillary; 11, point of maximum anterior constriction of squamosal root of zygomatic arch; 12, inferior most point of zygomatic arch; 13, posterior most point of zygomatic arch; 14, upper concave curve point of tympanic bulla; 15, superior most point of tympanic bulla; 16, posterior most point of tympanic bulla; 17, posterior most point of occipital; 18, anterior junction of maxillary and the frontal sutures. **C**, Ventral view: 1, anterior border of incisive foramen; 2, posterior border of incisive foramen; 3, posterior midline suture of palatines; 4, midpoint of suture between basisphenoid and basioccipital; 5, anterior alveolar margin of the upper molar row, at maxillary; 6, posterior alveolar margin of the upper molar row at palatines; 7, posterior border of ectotympanic part of auditory bulla; 8, posterior border of ectotympanic part of auditory bulla; 9, anterior most point of inferior margin of foramen magnum; 10, posterior most point of superior margin of foramen magnum; 11, Posterior inferior tip of squamosal root of zygomatic bar; 12, internal more concave curve point of inner extreme curvature of squamosal root of zygomatic arch; 13, superiormost margin of zygomatic arch; 14, posteriormost margin of the maximum anterior constriction of squamosal root of zygomatic; 15, internal more concave curve point of maxillary root of zygomatic arch; 16, external border of maxillary root of zygomatic arch.

The Procrustes-based geometric morphometric analysis is frequently used by researchers to analyze phenotypic distinctiveness of compared groups mainly based on cranial variation (Cardini, 2014). The basic idea of this method is the possibility of comparing the phenotypic characteristics through the cranial shape and size analysis (Cardini and Elton, 2009). Thereby, the standard linear

measurements are not used between specific marked points on the desired structure; instead, the Cartesian coordinates of the points (landmarks) are used. The amount or value of these points are analyzed using multivariate analysis, which are called "Shape variables". For taking pictures, a digital camera (Nikon P500) was fixed on a photography stand, parallel to the ground surface. Pictures taken in the

same standard conditions were saved in JPEG format.

Image digitizing and coordinate capturing was done using the software TpsDig2 ver.2.10, following the creation of the Tps file using TpsUtil ver.1.33 (Renaud and Michaux, 2007). In total, 16 landmarks were pointed for ventral, 12 for dorsal and 18 for lateral view of the skulls (Fig. 3).

After superimposition step in PAST (Paleontological statistics) version 3.14 using Generalized Procrustes Analysis (GPA) separate size and shape variation (Adams *et al.*, 2004), Principal component analysis (PCA) was used to get shape variables or PC scores to execute complementary statistical analysis such as Canonical Variate Analysis (CVA), PCA, Discriminant analysis (DA). Thin-plate spline was used to map the shape deformation from one object to another (Rohlf, 2010). Cluster analysis and analysis of similarities (ANOSIM) was used to find initial specimens' grouping. Canonical Variant Analysis was used in order to find significant differences between considered groups (Rohlf, 2006). In fact, the objective of this test is to separate or maximally distinguish two or more natural, a priori defined group of individuals. CVA maximizes the ratio of between group (among) to within group variance (Renaud and Michaux, 2007). In addition, this method can be used to determine the relationship between unknown-origin individuals and known populations (Louis and Diethard, 2011). CVA was also applied to analyze samples' covariance matrix to determine whether the predefined groups differ in terms of morphological characters or not, as well as to find the axes justifying the largest changes between the considered groups. For clustering individuals without a prior distinction of groups, principal component analysis (PCA) and cluster analysis (CA) can be used. The latter calculates distances between individuals and/or clusters in various ways while PCA is mainly based on combination of observed variables and data reduction. The goal of PCA is to summarize a multivariate dataset as accurately as possible using a few components.

Nonparametric MANOVA (NPMANOVA) with 10,000 permutations (p-values Bonferroni corrected) was performed to show groups distinctiveness in more details based on Euclidean distances. Using Mont Carlo randomization method, we compared Euclidean distances between paired groups.

In view of the fact that the classification of the specimens in three views of lateral, dorsal and ventral yielded somewhat similar results, thus only resulted graphs of the ventral view have been presented. Fortunately, errors that may occur during data collection, including the setting error (photographing error) and pointing error (landmarks setting error) are correctable; therefore, it is

necessary to select a subset of the samples with the aim of measuring the errors mentioned above prior to the analysis. Regarding the potential difference between the errors, they were analyzed separately based on Adriaens (2007). All obligatory assumptions of the statistical analysis such as data normality distribution were checked. All mentioned analyses were conducted in Morpho J, PAST and SPSS software.

Table II.- NPMANOVA results indicating pairwise comparison of the groups based on Euclidean distances (p-values for all data is < 0.05).

Pairwise groups	Euclidian distances between groups		
	Skull dorsal view	Skull ventral view	Skull lateral view
Eastern-Central and Western Iran	11.23	16.40	25.14
Iran-Europe	9.317	14.09	17.94
Iran- Caucasus	4.163	4.508	7.372
Iran- Krasnodar	9.273	12.19	11.73
Iran- Macedonia	10.32	14.08	19.51
Iran- Serbia	13.79	12.93	20.63

Table III.- The results of One-way ANOSIM (R values) and One-way PERMANOVA (F values) in comparing Iranian groups (P value <0.05 for all paired comparisons).

	Heiran		Kalaleh		Ramsar		Siahkal	
	R	F	R	F	R	F	R	F
Heiran			0.1807	2.92	0.0871	1.98	0.1142	1.60
Kalaleh	0.1807	2.92			0.1150	2.05	0.1789	2.08
Ramsar	0.0871	1.98	0.1497	2.05			-0.0165	0.80
Siahkal	0.1142	1.60	0.1789	2.08	-0.0165	0.80		

RESULTS

Based on the initial cluster analysis and previous molecular studies, we grouped all specimens in six major groups including Hyrcanian forests of northern Iran (including three sub groups of eastern, western and central parts of Hyrcanian forests), Europe, Caucasus region, Russia, Macedonia and Serbia. Pairwise comparison performed on all data (skull ventral, dorsal and lateral views) indicated that the Iranian populations (lineages) were significantly diverged from other populations (based on NPMANOVA analysis and Monte Carlo randomization and Bonferroni-corrected p-values) and that the population in eastern Hyrcanian forests of northern Iran is distinct from the population located in central and western parts of the Hyrcanian forests of the country (Table II).

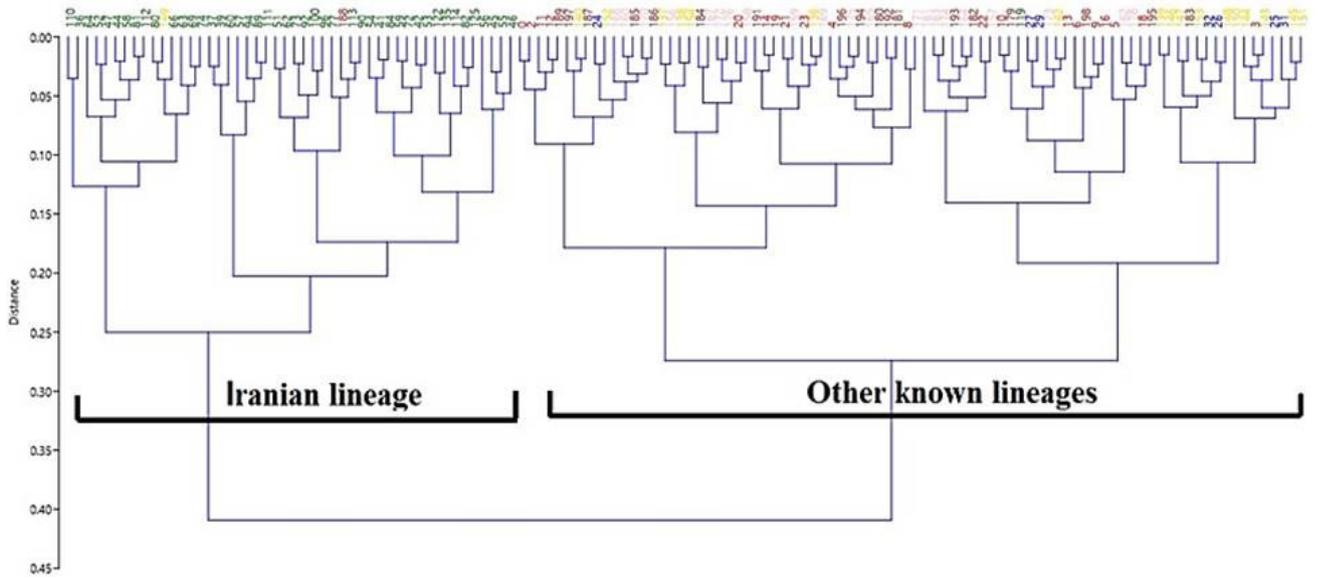


Fig. 4. Clustering tree indicates that the Iranian lineage separated considerably from other lineages (ventral view).

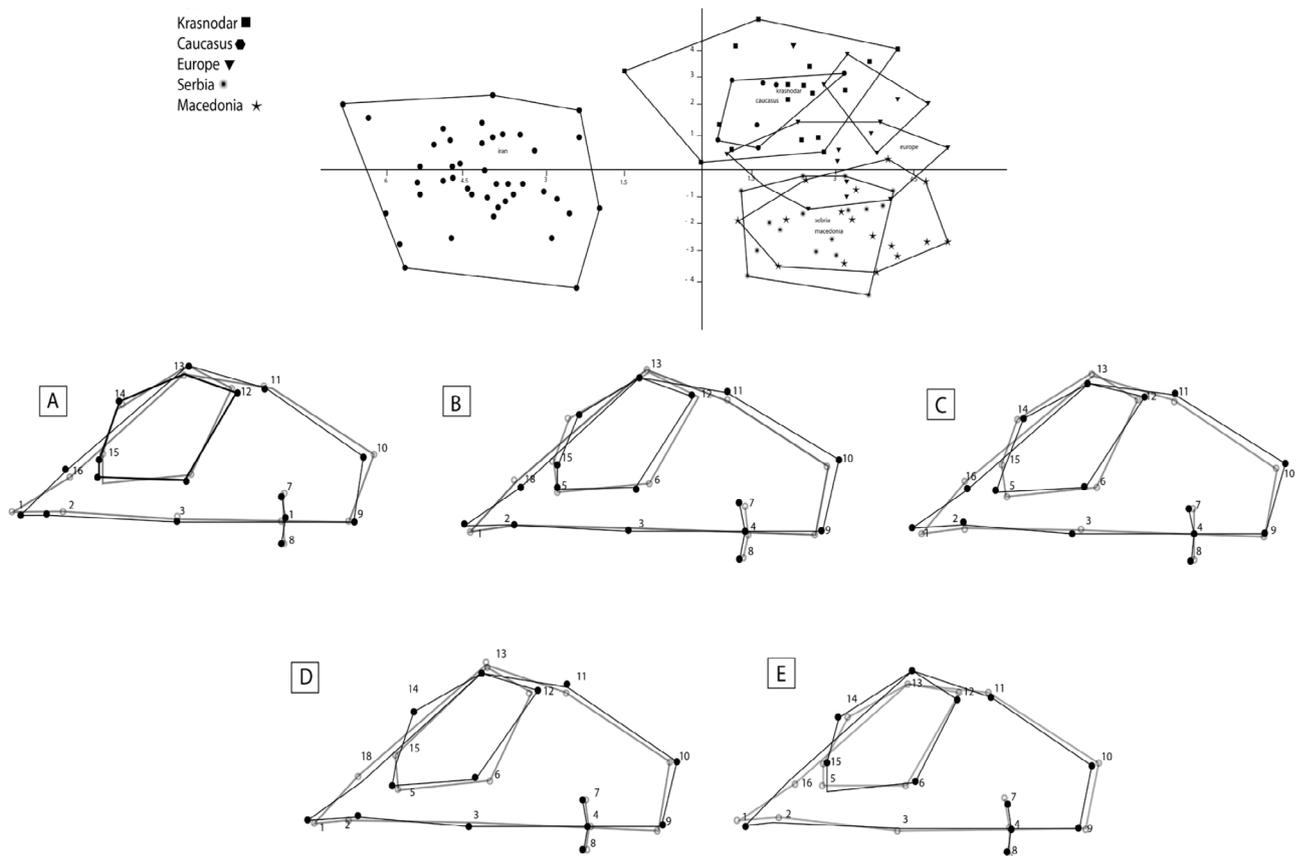


Fig. 5. CVA analysis shows the separation of the Iranian lineage from others (two first axes justify more than 90% of variances (ventral view)). A, Iran & Caucasus; B, Iran & Krasnodar; C, Iran & Macedonia; D, Iran & Europe; E, Iran & Macedonia. Darker line shows Iranian specimens and lighter one indicates others.

Cluster analysis (Fig. 4), CVA and Discriminant analysis confirmed considerable distinction of the Iranian lineage from other known lineages (Figs. 5, 6, 7).

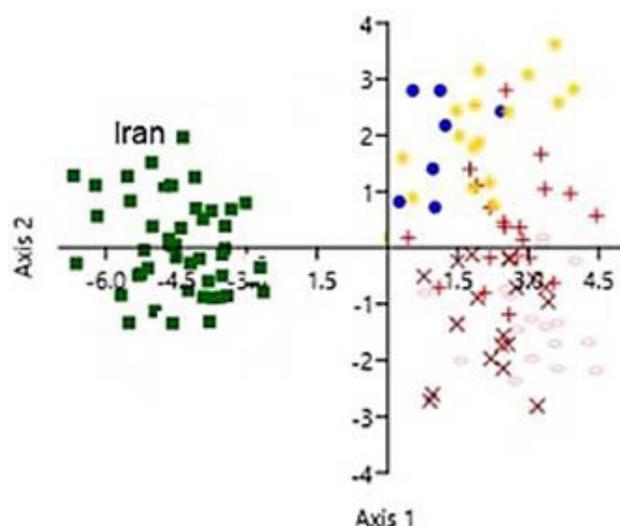


Fig. 6. DA analysis which shows the separation of the Iranian lineage from other lineages (two first axes justify more than 96% of variances for ventral view).

All samples were arranged into two groups, including northern Iran Hyrcanian populations and the remaining known lineages. Moreover, CVA showed complete discrimination of Kalaleh population (hereafter Kalaleh lineage) from central and western Iranian populations

(Fig. 8), also confirmed by One-way analysis of similarities (One-way ANOSIM) and One-way PERMANOVA (Table III). The results of the one-way PERMANOVA analysis for comparing Iranian groups as a whole with the other known lineages (groups) are presented in Table IV. Our analyses also showed that the two populations located in the extreme parts of northern Iranian forests, Kalaleh and Heiran regions, completely diverged from central Iranian populations (or known Iranian lineage) and can be considered as a new lineage which has not been published previously. The morphological divergence of the Kalaleh population is more considerable than other populations based on the skull morphology as well as other parameters like mean body weight, total body and tail length.

Table IV.- The results of One-way PERMANOVA (F values) in comparing Iranian lineages as a whole and other groups from ventral view (P value <0.05 for all paired comparisons).

	Eur	Cac	Ir	Kr	Mac	Ser
Europe		2.33	14.09	4.22	3.08	2.92
Caucasus	2.33		4.50	0.86	3.08	3.11
Iran	14.09	4.50		12.19	14.08	12.93
Krasnodar	4.22	0.86	12.19		4.82	5.38
Macedonia	3.08	3.08	14.08	4.82		1.54
Serbia	2.92	3.11	12.93	5.38	1.54	

Eur, Europe; Cac, Caucasus; Ir, Iran; Kr, Krasnodar; Mac, Macedonia; Ser, Serbia.

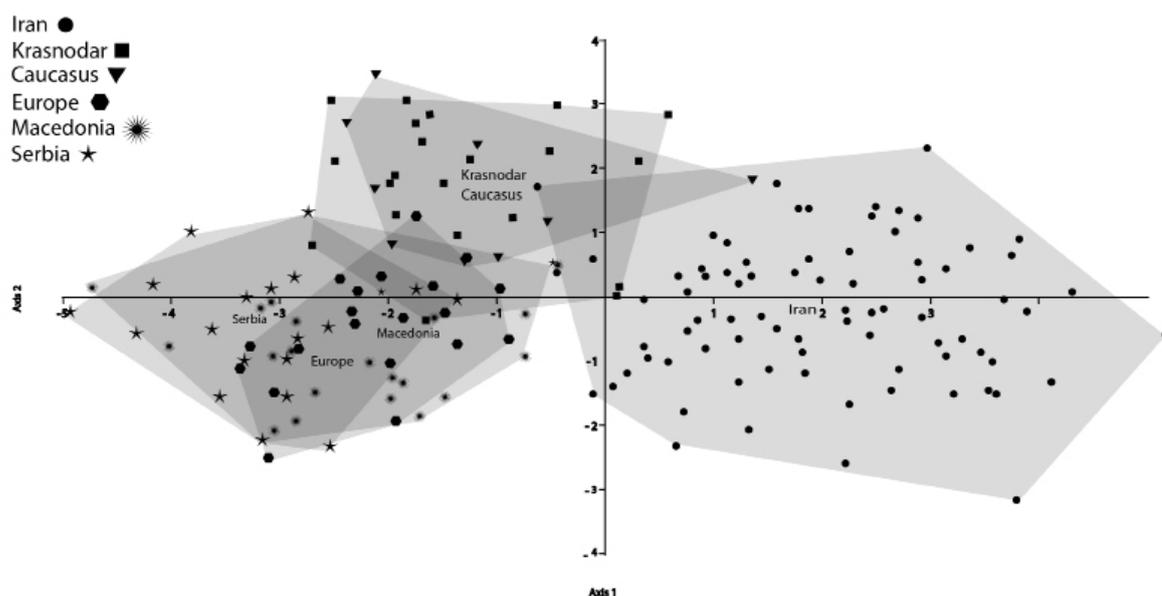


Fig. 7. TCVA analysis which indicates the separation of Kalaleh lineage from other Iranian populations (two first axes justify more than 87% of variances (ventral view) but Heiran population is the same (also distinct). For more details, see Figure 5.

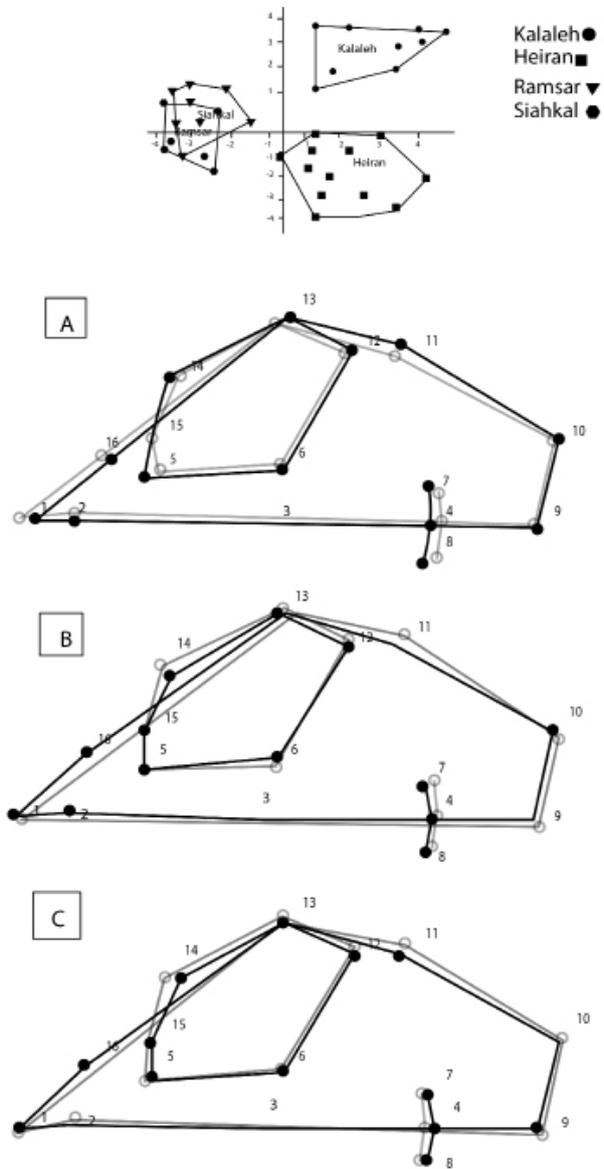


Fig. 8. CVA analysis which shows the separation of Kalaleh lineage from other Iranian populations (two first axes justify more than 87% of variances (ventral view) but Heiran population is the same (also distinct). For more details, see Figure 5.

Multivariate ANOVA also confirmed that the Iranian lineage (or lineages) shows apparent distance from the other groups (MANOVA: $F_{x,y} = 23.6, P < 0.0001$), similar to the findings of ANOVA performed on centroid size data, as well as results of Tukey post hoc test ($P < 0.001$) (Table V).

CVA also gained the same results and produced three main axes justifying more than 90.07%, 81.56% and 84.55% of variances, respectively (Supplementary Table I). Supplementary Table II shows the significant

level of the morphological differences between the defined groups.

Table V.- NPMANOVA results indicating pairwise comparison of the groups based on Euclidean distances. The values in the parenthesis shows p-values.

Pairwise groups	Euclidian distances between groups		
	Skull dorsal view	Skull ventral view	Skull lateral view
Eastern Central and Western Iran	11.23	16.40	25.14
Iran-Europe	9.317	14.09	17.94
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DISCUSSION

All multivariate statistical analyses confirmed that the Iranian lineage shows high cranial morphological divergence from other known lineages all over the species distributional range. Furthermore, Iranian populations have experienced distinct evolutionary forces, which led to the separation of the eastern population from central and western parts. As molecular investigations done by Naderi et al. (2013, 2014) shows the molecular distance between the Iranian eastern population and other Iranian populations is greater than the distance between the Iranian lineage as a whole and the European lineage. Such investigations also reported that the statistical distance between the lineages is much higher than the maximum intra-specific distance recorded for rodents (Naderi et al. 2013, 2014). Integrating our findings with previous molecular results, we believe that the phylogeny of *G. glis* is more diverse than what was previously known. It seems that the Fat dormouse passed a separate evolutionary path because of the long-term survival with no contact with other populations of the western Palearctic range. We also concluded that skull morphology could be used as a complementary method in similar evolutionary divergence studies on rodents. Bones of the skull and mandible of many rodents are investigated in studies on the evolution of complex morphological structures because they show morphological evolutionary changes in rodents better and more quickly (Zhao and Yang, 1997).

The advent of at least two unique lineages of this species in northern Iran Hyrcanian forests can be attributed to climatic, topographic and niche divergence along the Hyrcanian forests based on molecular findings (Naderi, 2014). The effects of such factors had been previously reported by different authors (Li, 1989; Claridge and

Gillham, 1992; Yao *et al.*, 2010). Other reasons for such patterns of divergence could be related to the dispersion barriers and ecological long-term traps in the Caspian forests of northern Iran. It is expected that the long-term survival of the species in this refugium and probably in micro-refugia along the Alborz mountainous ridges led to completely distinct evolutionary processes compared to other parts of the Palearctic biogeographic region. Previous studies on the basis of identified phylogenetically-distinct lineages of *G. glis* and cryptic patterns of diversification introduced the Hyrcanian Forests as a monotonic glacial refugium (Ramezani *et al.*, 2008). Our study reveals major niche differentiations among novel phylogeographic lineages of *G. glis*, which helps elucidate the niche conservatism theory. Having relatively the longest hibernation among mammalian species and limited time for feeding, emphasis on the importance of the mast yield in the Hyrcanian forests. Recently, Ahmadi *et al.* (2018) concluded that climatic variables affecting habitat production are the most influencing factors on intraspecific isolation of cryptic species. However, phenotypic variation cannot be simply attributed to direct genetic documents, but also considerable morphological changes in different parts of the skull can be regarded as reliable tools for evolutionary inferences. Our results clearly confirmed that intraspecific skull morphological variations correspond to species niche characteristics in different parts of the study area. Some of these variations appear to be driven by drier climates (Gienapp *et al.*, 2008; Pergams and Lawler, 2009) and shorter growing seasons (Ward *et al.*, 2000) in the most eastern parts of the Hyrcanian forests.

This study suggests a relatively severe gradient of morphological changes between the populations studied in Iran and elsewhere in the world. Identical morphological findings as those seen in previous molecular findings showed that the Iranian lineage had experienced distinct evolutionary forces while trapping in a relatively isolated Hyrcanian refugium and divided to at least two potential lineages including the Iranian eastern lineage and the Iranian western lineage. Based on previously published data regarding intraspecific genetic distances of more than 12% for the Iranian lineage (Naderi *et al.*, 2013), as well as the extensive morphological divergence of Iranian specimens from other populations distributed in the Palearctic region, we suggest that a taxonomic revision based on complementary investigations such as using nuclear markers can result in interesting findings on the species taxonomic position. Such clearly morphological changes corresponding to the molecular markers can be used as an ideal model to initiate long-term investigations (Michaux *et al.*, 2007) on the consequences of the global climate change and conservation of biodiversity in the future.

ACKNOWLEDGMENTS

We would like to thank Dr. Boris Krystufek who proposed the first idea of previous researches on the phylogenetic situation of the species. His advice on the various stages of the research led to the idea of our morphological investigations. Thanks to Mr Masoud Lahout, Mehdi Kamran and Afshin Davarpanah who helped us in the field work. Special thanks to the colleagues from St Petersburg zoological museum, Vladimir G. *Malikov*, Alexandra Davydova and Fedor Golenishchev.

Supplementary material

There is supplementary material associated with this article. Access the material online at: <https://dx.doi.org/10.17582/journal.pjz/2020.52.1.337.346>

Statement of conflict of interest

The authors declare no conflict of interest.

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