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PHYLOGEOGRAPHY OF AN ANATOLIAN ENDEMIC AND ALPINE SPECIALIST WOOLLY DORMOUSE (*Dryomys laniger*) WITH A DESCRIPTION OF A NEW SPECIES

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Abstract

The genus Dryomys, represented by four species, spreads a variety of habitats, including forests and mountains. The Wooly Dormouse (Dryomys laniger) is a rock-dwelling alpine species endemic to South and Central Anatolian mountains. No targeted study has been conducted to explore the full distribution area of this species nor to reveal the phylogenetic structure within the species. We used CYTB and IRBP as a molecular marker to see intraspecific diversity of the species. Besides this, morphological characters are used to reveal differences between the populations. Phylogenetic trees showed that Dryomys laniger has two different mtDNA clades, each with a distinct distribution range. The representatives of the most distinct clade also have a number of shared and distinct morphological features, and we hereby describe it as a new endemic species Dryomys anatolicus sp. nov. The other clade comprises two different clades. Despite considerable molecular differences between the two clades, we could not find any difference in morphology. Two endemic species have a complex history in Anatolia starting in the late Oligocene epoch. In that era, the ancestors of Dryomys laniger and Dryomys anatolicus separated from Dryomys nitedula and started to adapt to high altitudes. Then complete divergence between the two species occurred at the beginning of the Pliocene. In this study, we suggest that geologic events and climate have a big role in speciation events between Dryomys laniger and Dryomys anatolicus.

1. INTRODUCTION

The genus *Dryomys* comprises four recognized species, each with distinct distribution ranges. *Dryomys nitedula* (Pallas, 1778) is notable for its wide distribution range. *Dryomys laniger* [1] is an endemic species found exclusively in the Taurus Mountains of Türkiye. *D. niethammeri* [2] is currently known only

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from Balochistan, Pakistan. Recently, a new species, *D. yarkandensis* [3], was described from Xinjiang, China.

The genus *Dryomys* is exclusively distributed within the Palearctic region and is characterized by a broad yet fragmented distribution pattern [4–8]. These mammals inhabit various habitats, primarily favoring mountainous regions, including forests. *Dryomys laniger*, commonly known as the Wooly dormouse, is a rock-dwelling species initially described in the western and central Taurus mountains [4]. Subsequently, additional populations were discovered in the eastern regions of Munzur and Palandöken mountains within Eastern Anatolia [9,10]. Notably, this species exhibits a patchy distribution, with all populations recorded at elevations exceeding 1600 meters. An interesting aspect of its behavior is that it undergoes a seven-month hibernation period, starting in the final week of October and lasting until the first half of April [11]. Despite this, our understanding of *D. laniger*'s biology remains limited, with the most comprehensive study conducted by Spitzenberger (1976). The most recent research regarding the species' distribution and biology was conducted by [12].

Until now, no specific studies focused on finding out the distribution area of the species. Instead, the information we have comes from general surveys of small mammals conducted by only a few researchers. No research has been conducted on the genetic diversity within this species or the structure of its populations, even though molecular studies have been carried out comparing it to other members of the genus *Dryomys* and the family *Gliridae* [13,14]. Only two studies [14,15] used mtDNA (12 rRNA and ND1) and nuclear DNA (Fib7) to compare two geographically close populations of *D. laniger* just from the central Taurus mountains.

Anatolia's geological events and climate have had a significant impact on species diversity and evolutionary history in the region. The Neogene surface uplift in Anatolia has affected the regional biota, particularly the diversity of plants and large mammals [16]. The interaction of geological and climatic changes can lead to speciation and dramatic redistribution of various group of the species across the complex landscape and the uplift of the Anatolian plateau has created new habitats and isolated populations, leading to the diversification of species [17–19]. The Late Quaternary changes have caused substantial geographic range shifts and phylogeographic breaks for various species in this region [20].

In light of the gaps in our knowledge highlighted earlier regarding the evolutionary history and geographical patterns of mammals in this region, this study aims to provide a comprehensive understanding of *D. laniger*'s phylogenetic relationships using the both mtDNA (*CYTB*) and nuclear DNA (IRBP) marker. We intend to address these limitations by clarifying the historical biogeographic processes that have shaped the species' distribution, elucidating the influence of past climatic fluctuations and geological events on population divergence, and identifying potential conservation units within *D. laniger*. Our research not only fills critical knowledge gaps but also forms a foundational basis

for future studies, aiding in the effective conservation and management of this species.

2. MATERIALS AND METHODS

2.1 Sampling

Field studies were carried out between 2015-2018. We identified and searched the high-altitude, rocky habitats previously described as characteristic of *D. laniger* [13,14,21]. A total of 31 samples were collected from 6 localities (Figure 1 and Supplementary Table S1). Animals were captured alive using Sherman traps. Since these samples were used in another zoonotic study, the animals were dissected and the liver tissues were stored in RNA-later solution. The skins, tissues and skulls of specimens examined were deposited in the Zonguldak Bülent Ecevit University. The procedure was approved by Zonguldak Bülent Ecevit University Animal Experiments Ethics Committee (permit no. 91330202-10).

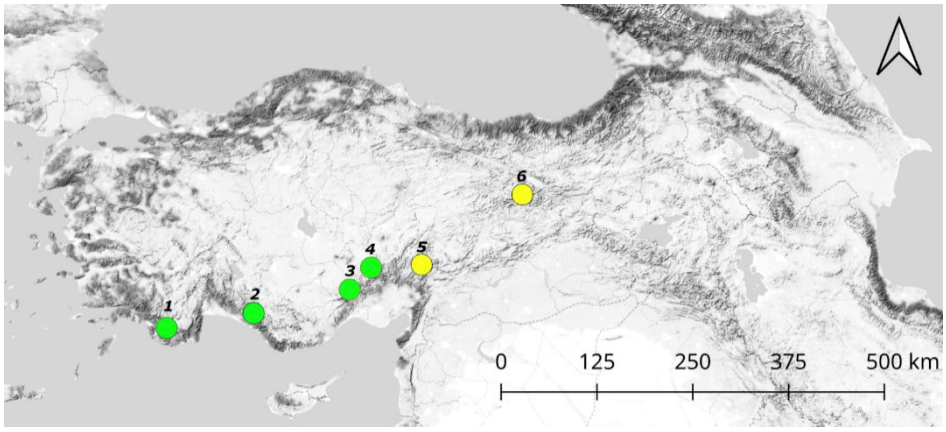

FIGURE 1. Distribution of *D. laniger* (Green) and *D. anatolicus* (Yellow). Numbers are indicate the localities of *D. laniger*; 1. Subaşı Plateau (Akdağ Mountain), 2. Salamut Plateau (Geyik Mountain), 3. Meydan Plateau Bolkar mountains, 4. Çiçekliboyun Plateau Aladağlar mountains; and *D. anatolicus*: 5. Püren Pass (Armut mountains) and 6. Eşekçayırı Plateau (Munzur mountains)

2.2 DNA isolation and amplification

Total genomic DNA was extracted from the liver using a DNAeasy extraction kit following the manufacturer's protocol (AMBRD Laboratories, Istanbul, Türkiye). The partial *CYTB* gene (1124 bp) was amplified and sequenced using the primers L7 (Forward): 5'-ACCAAT-GACAT-GAAAAATCATC GTT-3' and H6 (Reverse): 5'-TCTC-CATTTCTGGTTTACA-AGAC-3'[22]. The PCR protocol for *CYTB* included: 5 min initial denaturation of 95°C, 30 sec denaturation of 95°C, 55 sec annealing of 60°C, and 90 sec extension of 72°C,

for 35 cycles, and a final 10 min extension of 72°C. The partial IRBP gene (1172 bp) was amplified and sequenced using the primers IRBP217 (Forward): 5'-ATGGCCAAGGTCCTCTTGGATAACTACTCGTT-3' and IRBP1531 (Reverse): 5'- CGCAGGTCATCATGATGAGCTTGCTCTGTGTTCTG-3' [23]. The PCR protocol for IRBP included: 5 min initial denaturation of 95°C, 60 sec denaturation of 94°C, 60 sec annealing of 55°C, and 180 sec extension of 70°C, for 30 cycles, and a final 10 min extension of 72°C. After the PCR step, we purified the PCR products with a PCR product purification kit following the manufacturer's protocol (AMBRD Laboratories, Istanbul, Türkiye). The purified PCR products were Sanger-sequenced by the Macrogen-Europe Inc. All sequences used in this study were uploaded to GenBank (Supplementary Table S1).

2.3 Phylogenetic reconstructions

The *CYTB* and IRBP sequences were checked visually, edited, and aligned using the ClustalW algorithm in GENEIOUS software [24]. Both datasets were used to reconstruct the phylogenetic position of the samples. In total, 29 samples for *CYTB* and 12 samples for IRBP were successfully amplified. To better understand the phylogeny of the genus *Dryomys* we use all the *D. nitedula* samples uploaded in GenBank, using all available *CYTB* sequences longer than 740 bp and IRBP sequences longer than 1110 bp. We also added *Eliomys quercinus* and *Eliomys melanurus* as outgroups (Details in Supplementary Table S2).

Phylogenetic relationships were reconstructed by Maximum Likelihood (ML) and Bayesian inference (BI) algorithms. Best fit models of molecular evolution were selected by MrModelTest 2 [25]. The best model was GTR + G + I for *CYTB* dataset and HKY + G + I for IRBP dataset. ML analyses were done in RaxmlGUI [26]. ML+rapid bootstrap were selected, the number of bootstrap replicates was set to 1000, and the duplicated sequences were not included for both datasets. The Bayesian inference (BI) algorithm was performed using MrBayes 3.2 [27]. Monte Carlo Markov chain (MCMC) searches in MrBayes were run with four chains in two separate runs for 20,000,000 generations with default priors, trees sampled every 1000 generations discarding the first 25% as burn-in for both dataset. The representatives of genus *Eliomys* were used as outgroups in each tree. FigTree v1.4.3. was used to visualize the phylogenetic trees. Mitochondrial haplotypes were identified using DnaSP 6 [28]. The number of haplotypes (h), number of segregating sites (S), haplotype diversity (Hd), the average number of nucleotide differences (K), and nucleotide diversity (pi) for *CYTB* were calculated in DnaSP 6 [28]. The mean genetic distances between *D. laniger CYTB* clades and *D. nitedula* subspecies were calculated using the Kimura 2 parameter distance (K2P) model in MEGA [29]. We used the TCS method [30] to draw both *CYTB* and *IRBP* haploytpe networks. Haplotype

networks of species drawn with POPART software [31]. The datasets used in the network analyses were constructed by removing outgroups. To evaluate the demographic history pattern of the populations of *CYTB* dataset mismatch distribution analysis were run with DnaSP 6 [28]. Analysis of molecular variance (AMOVA) for *CYTB* dataset was conducted in Arlequin ver 3.5.2.2 to see variation among groups [32]. Divergence times were estimated in BEAST 2 [33] for *CYTB* dataset based on two calibration points: (1) the split between *Eliomys*/*Dryomys* which is 28.5 mya (± 2.8) and (2) divergence between two *E. quercinus* and *E. melanurus* around 7.0 mya (± 0.9) [34]. The best model chosen for the analysis was the strict clock and the calibrated Yule model tree prior. The MCMC chains were run for 50 million generations, sampled every 1000 generations. Posterior distributions of the parameter estimates were evaluated by monitoring the effective sample size (ESS >200) and trace plots in Tracer 1.6 [33]. TreeAnnotator was used to summarize the trees and the first 25% of trees were discarded as burn-in. The phylogenetic trees with divergence times were displayed in FigTree v1.4.3.

2.4 Morphometry

Skulls and mandibles were photographed for morphological evaluation. Beside our dataset we also add *D. nitedula* (n=6) museum specimens deposited in Zonguldak Bülent Ecevit University. External characters, skulls and mandibles were used for linear morphometric analyses and skulls (dorsal and ventral) and mandibles were used for the geometric morphometric analyses (Table 1). Due to possible shape changes that may arise from young individuals, these individuals were not included in the analyses.

TABLE 1. Number of samples used for both linear and geometric morphometry

	Linear morphometry		
	External characters	Skulls	Mandibles
D. laniger	n=20	n=10	n=10
D. anatolicus	n=11	n=10	n=10
D. nitedula	n=6	n=6	n=6
	Geometric morphometry		
	Skull (Dorsal)	Skull (Ventral)	Mandibles
D. laniger	n=10	n=10	n=10
D. anatolicus	n=7	n=6	n=9
D. nitedula	n=5	n=6	n=4

2.4.1 Linear morphometry

For use in morphological evaluation four external characters, head and body (HB), tail length (TaL), length of the hindfoot (HF), and length of the ear (EL), and weight (in grams) were measured following [35]. Skulls and mandibula were measured following [35]) and Krystufek and Vohralík (2005). For the analysis, a total of 33 morphological characters were measured, including 28 skulls and mandibles and 4 external characters, as well as the weights of the samples. Minimum values, maximum values, mean values and standard deviation values of a total of 32 characters and body weight obtained from *Dryomys* samples were recorded (Supplementary Table S3). All measurements were measured with Vernier caliper (to the nearest 0.1 mm) and then re-measured under a stereomicroscope to double check. The results were recorded for linear morphometric analysis. All measurements were given in millimeters and body weight in grams (0.1 grams) (as given below). **ZB**— zygomatic breadth; **RW**— rostrum width; **IC**— interorbital constriction; **OL**— occipito-nasal length; **NL**— nasal length; **NW**— nasal width; **FSL**— lenght of frontal suture; **PSL**— length of parietal suture; **OW**— occipital width; **BW**— braincase width; **CBL**— condylobasal length; **CNL**— condylonasal length; **BL**— basal length; **FRL**— length of facial region; **MB**— mastoid breadth; **BCL**— braincase lengh; **DL**— lenght of diastema; **PL**— palatal length; **FI**— lenght of foramen incisivum; **ABL**— auditory bullae length; **ABW**— auditory bullae width; **MTL**— length

of maxillary tooth row; **RH—** rostrum height; **BBL—** lenght of braincase with bullae; **BOL—** lenght of braincase without bullae; **MATL—** length of mandibular tooth row; **HL—** height of mandibula; **ML—** length of mandibula; **BW—**body weight; **EL—**length of ear; **HFL—**length of hindfoot; **TL—**length of tail; **HBL—**length of head and body.

Principal Component Analysis (PCA), Bivariate and Multivariate analysis were performed to reveal how the species were grouped and the effects of variations on the groups. IBM SPSS 26 program (IBM SPSS 26) was used for statistical analysis.

2.4.2 Geometric morphometry

The skull (dorsal, ventral) and mandible of the samples were captured with Canon R6 MII camera and the images were analyzed in accordance with the geometric morphometric procedure [36,37]. The TpsUtil software was used to edit the skull and mandible images in which landmark points were placed and to set the file formats [38]. Landmarks (LMs) were deposited on the same plane for all samples. Two-dimensional landmarks, which will enable the identification of shapes, were digitized with the tpsDig program [39]. 14 landmarks were used for the dorsal side of the skull, 19 landmarks for the ventral side and 13 landmarks for the mandible. Landmarks were placed on the right side only (Figure 2).

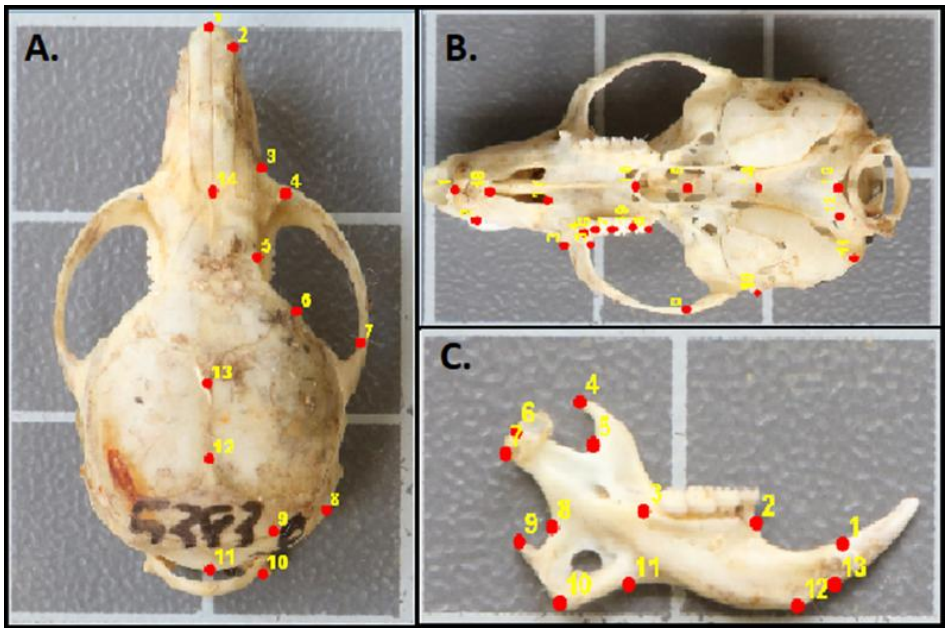

FIGURE 2. Landmark location on *Dryomys* skull. (A: Dorsal Cranium; B: Ventral Cranium; C: Mandible)

Boxplots were used to show differences between groups [40]. The significance of differences in central dimension was tested by analysis of variance. ANOVA test was performed with the help of PAST v.4.03 software [41].

Generalized Procrustease Analysis (GPA) eliminated margins of error before distributing the samples, enabling more accurate results in shape and size comparisons [36,40]. The MorphoJ software was used for the GPA [42]

Species groups were determined genetically before analyses. Principal Component Analysis (PCA) and Canonical Variate Analysis (CVA) were then performed to identify the shape diversity in the samples. Patterns of shape changes in the skull and mandible were investigated using PCAs due to variance-covariance matrices. CVAs were used to statistically distinguish groups. Discriminant Function Analysis (DFA) revealed the distinction between the two groups. The MorphoJ software used to perform the analysis [42].

3. RESULTS

3.1 Molecular analysis

All examined geographical populations of *D. laniger* split into two phylogenetic clades (Green Clade and Yellow Clade), each with strong support in *CYTB* dataset (Figure 3). The green clade comprises two clades, Clade 1; Subaşı plateau (Akdağ Mountain) and Salamut plateau (Geyik Mountain) in Western Taurus mountains. Clade 2 from the Central Taurus mountains includes populations from Meydan (Bolkar mountains) and Çiçekliboyun (Aladağlar mountains) plateaus. The yellow clade includes two populations one from Püren pass (Armut mountains) and the other one from Eşekçayırı plateau (Munzur mountains). There is a deep divergence between green clade and yellow clade, strongly supported in both BI and ML phylogenetic analyses which show the same tree topology. Regarding the phylogenetic tree constructed using the IRBP dataset, it also displays the presence of two separate clades (Green and Yellow clades). BI and ML phylogenetic analyses show the same tree topology (Figure 4).

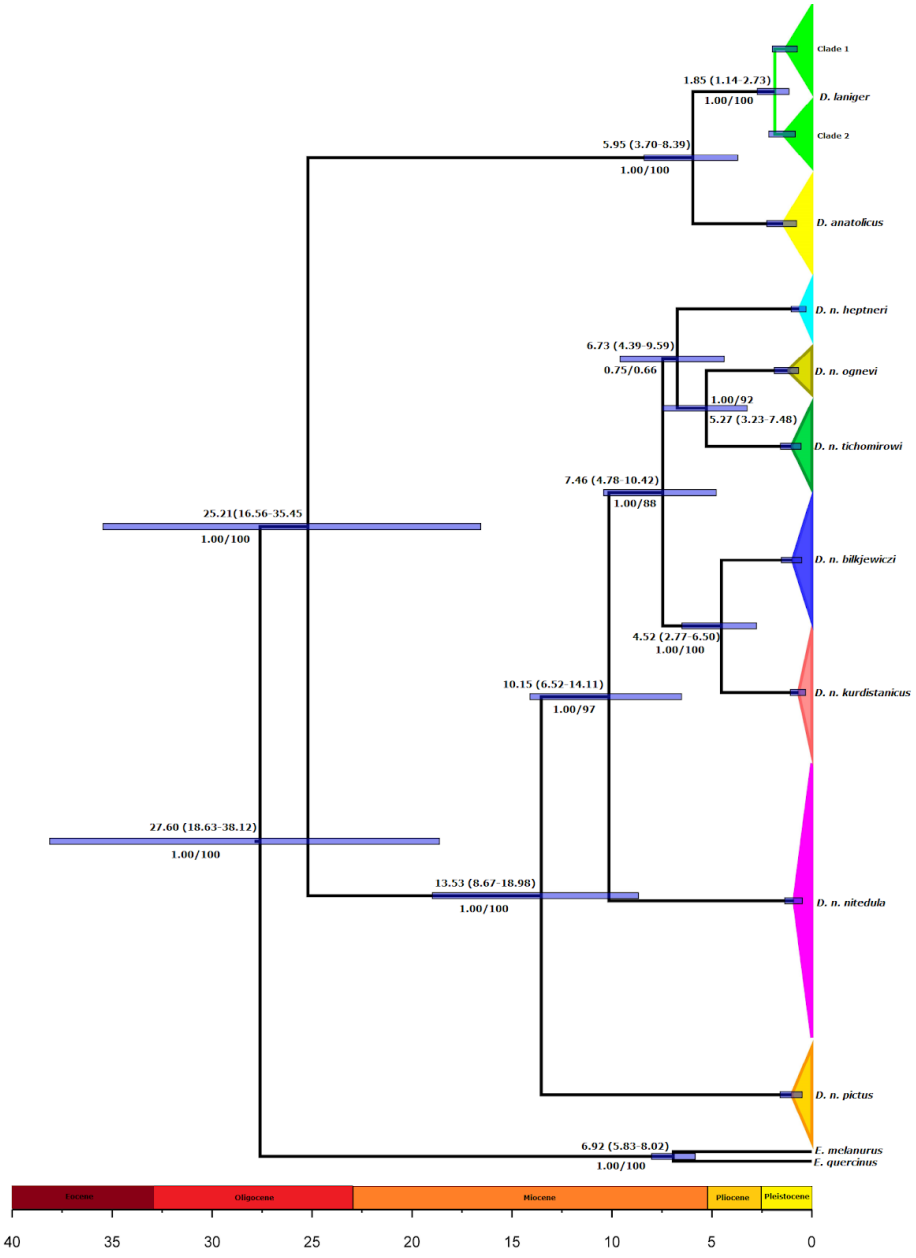

FIGURE 3. Phylogenetic relationships and divergence time based on *CYTB*. Numbers at nodes show posterior probabilities and bootstrap values for Bayesian (left) and ML inference (right), respectively. The blue bars represent the 95% HPD interval

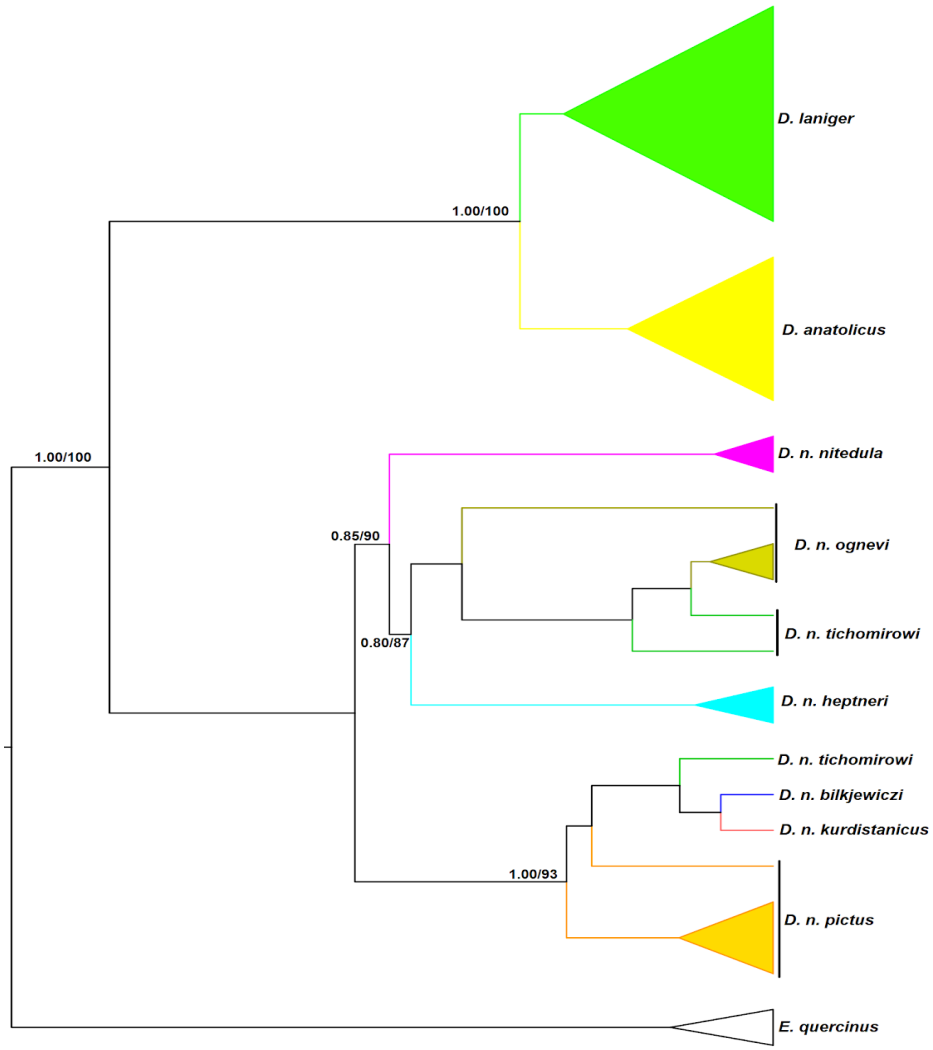

FIGURE 4. Phylogenetic relationships based on IRBP. Numbers at nodes show posterior probabilities and bootstrap values for Bayesian (left) and ML inference (right), respectively

We identified 17 unique haplotypes in *D. laniger* populations (no haplotypes were shared between clades: Supplementary Table S4). Genetic diversity analyses of two clades of green clade and yellow clade showed that the latter has low diversity compared to green clade (Table 2).

TABLE 2. Genetic differentiation of *D. laniger*'s two clades and *D. anatolicus* based on *CYTB*. Number of individuals (N), number of segregating sites (S), number of haplotypes (h), haplotype diversity (Hd), average number of differences (K) and nucleotide diversity (Pi)

	N	S	h	Hd	K	Pi
Dryomys laniger						
clade 1	10	33	8	0,956	13,33	0,012
clade 2	8	36	7	0,964	11,07	0,010
Dryomys anatolicus						
	11	19	2	0,545	10,36	0,009

The haplotype network (Figure 5) of *CYTB* reveals a substantial number of nucleotide substitution differences between two clades of *D. laniger*, clade 1 and clade 2 differ by 93 bases from *D. nitedula* clade and 27 bases from yellow clade. K2P distances between two clades of *D. laniger* and *D. nitedula* subspecies; clade 1 and clade 2 are the closest to each other (1.9%), and clade 1 and yellow clade are the most distant (7.2%). *D. n. nitedula* is the furthest (24.3% with both clade 1 and clade 2, 24.8% with yellow clade) and *D. n. kurdistanicus* is closest (19.9% with clade 1, 20.5% with clade 2, 21.1% with yellow clade). (Supplementary Table S5).

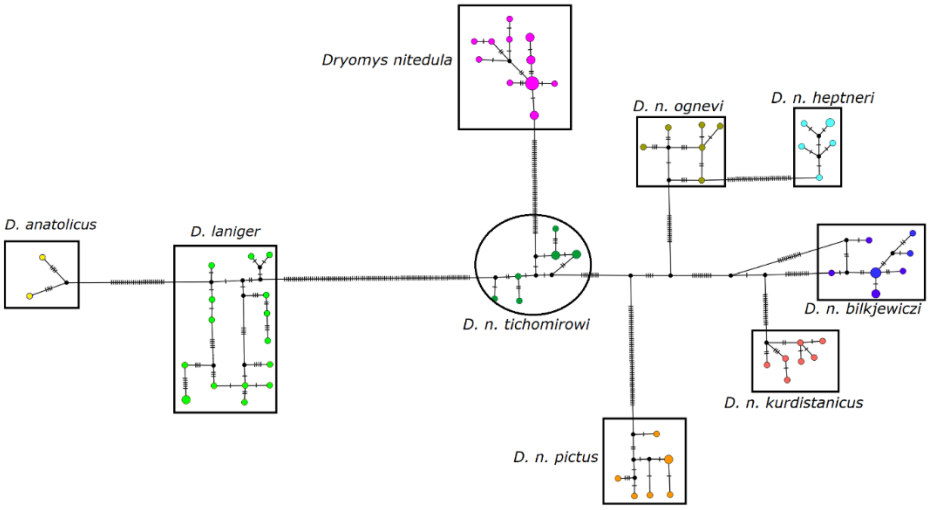

FIGURE 5. Haplotype network based on *CYTB*

The mismatch distribution of *D. laniger* is multimodal and *D. anatolicus* is bimodal (Figure 6). AMOVA shows that populations are significantly and genetically different from one another which revealed that the greatest amount of genetic variation occurred among populations (80.63%) and the p-value of the FST is p = 0.000 (P <0.05) (Figure 7).

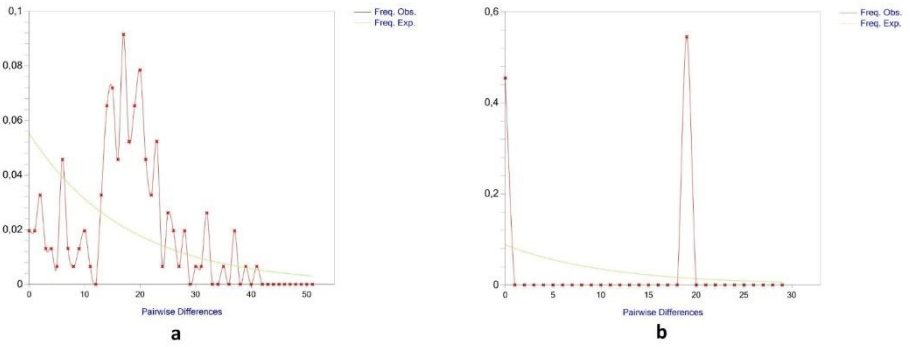

FIGURE 6. Mismatch distributions for a) *D. laniger* and b) *D. anatolicus*

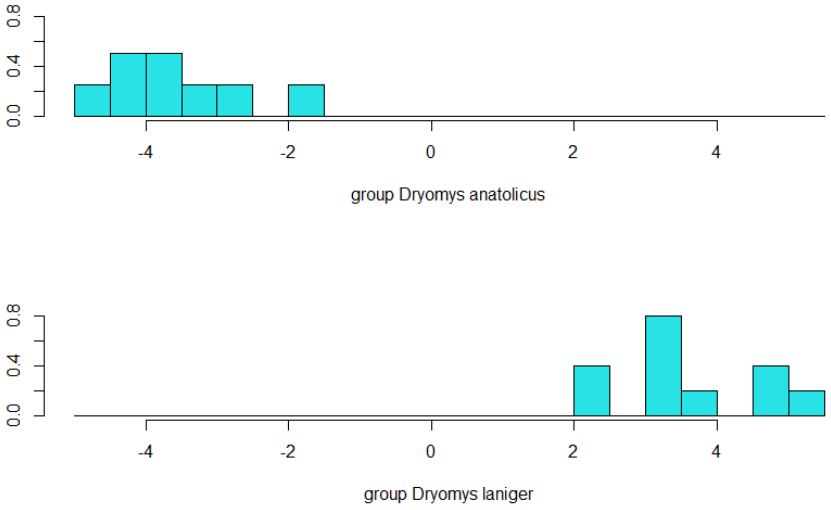

FIGURE 7. AMOVA results between *D. laniger* and *D. anatolicus*

According to our divergence time estimates, *D. nitedula* and *D. laniger* separated from each other by ~25.21 mya (HPD: 16.56 – 35.45 Mya). The split between green clade and yellow clade was dated at ~5.95 mya (HPD: 3.70 – 8.39 Mya). Within the green clade, clade 1 and clade 2 diverge 1.85 mya (HPD: 1.14 – 2.73 Mya) (Figure 3).

3.2 Morphometry

3.2.1 Linear morphometry

The genetic lineages of the *Dryomys* species samples used in morphological analysis have been previously determined and are also shown in phylogenetic analysis based on *CYTB* (Figure 3). According to the PCA analysis performed for 4 external characters and body weight data, three main components were formed and explained 81.17% of the variations. All of the variables of the main components were positively correlated (loading >0.399, loading >0.775, loading >0.573) and accounted for 32.90%, 26.11% and 22.15% of the variation, respectively (Table 3).

TABLE 3. Factor data (based on 4 external characters and body weight) variables of two main component axes of *Dryomys* species

Variables	**FAC1**	**FAC2**	**FAC3**
HBL	—	0.859	—
TL	0.890	—	—
HFL	0.680	—	0.573
EL	—	—	0.930
BW	0.399	0.775	—
Eigenvalue	1.645	1.306	1.108
Explained variance (%)	32.902	26.112	22.154

According to multivariate and bivariate analyses; HFL and TL characters were selected for the X and Y axis. Looking at the distribution graph of the species after the selected characters, it was seen that *D. nitedula* was clearly separated from the other two species, and the samples of *D. anatolicus* and *D. laniger* were clustered together, except for a few samples representing the species (Figure 8a).

According to the PCA analysis performed for 28 skull and mandible character data, two main components were formed and explained 3.80-81.51% of the variations. All variables in PC1 and PC2 were positively correlated (loading >0.409 and loading >0.345) and accounted for 81.51% and 3.80% of the variations, respectively (Table 4).

TABLE 4. Factor data of the two principal components axes (Based on 28 skull and mandible variables of *D. anatolicus*, *D. laniger* and *D. nitedula*)

Variables	**FAC1**	**FAC2**
NW	0.687	0.619
FSL	0.608	0.649
PSL	0.907	—
OW	0.817	0.534
MATL	0.780	0.560
RW	0.788	0.581
IC	0.761	0.530
NL	0.675	0.646
FRL	0.661	0.468
DL	0.627	0.632
PL	0.409	0.785
FI	0.606	0.664
MTL	0.843	0.499
ZB	0.786	0.571
RH	0.791	0.578

HL	0.791	0.590
BW	0.890	0.376
ABL	0.647	0.622
BBL	0.899	0.347
BOL	0.905	0.345
ABW	0.788	0.513
BCL	—	0.764
CNL	0.798	0.415
CBL	0.631	0.696
ML	0.680	0.577
OL	0.626	0.624
BL	0.770	0.393
MB	0.855	0.359
Eigenvalue	22.823	1.064
Explained variance (%)	81.512	3.799

According to multivariate and bivariate analyses; NW, FSL, PSL, PL were selected for the X and Y axes from the skull characters and MATL from the mandible characters. According to the distribution graphs created after the selected skull and mandible characters, it was seen that *D. nitedula* was clearly separated as in the external characters. However, it was determined that the samples belonging to *D. anatolicus* and *D. laniger* were clearly separated from each other except for a few samples representing the species. Morphological analysis shows that *Dryomys* species are distinguished based on skull and mandible variables (Figure 8b).

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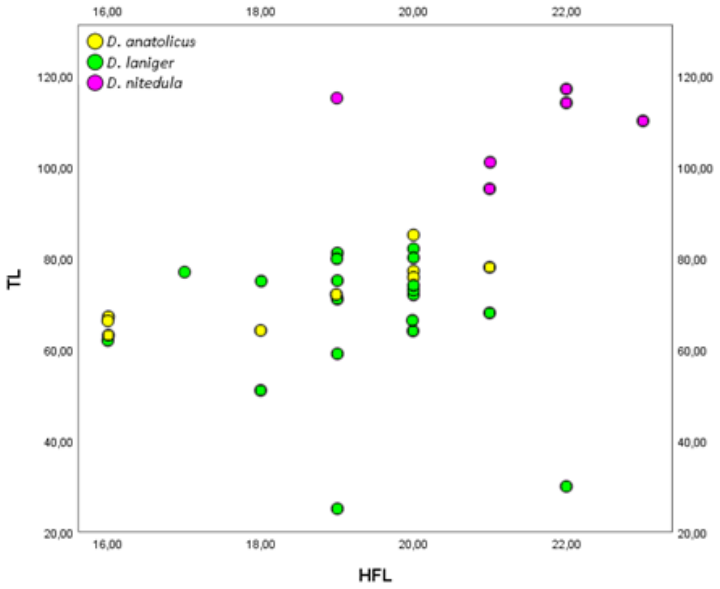

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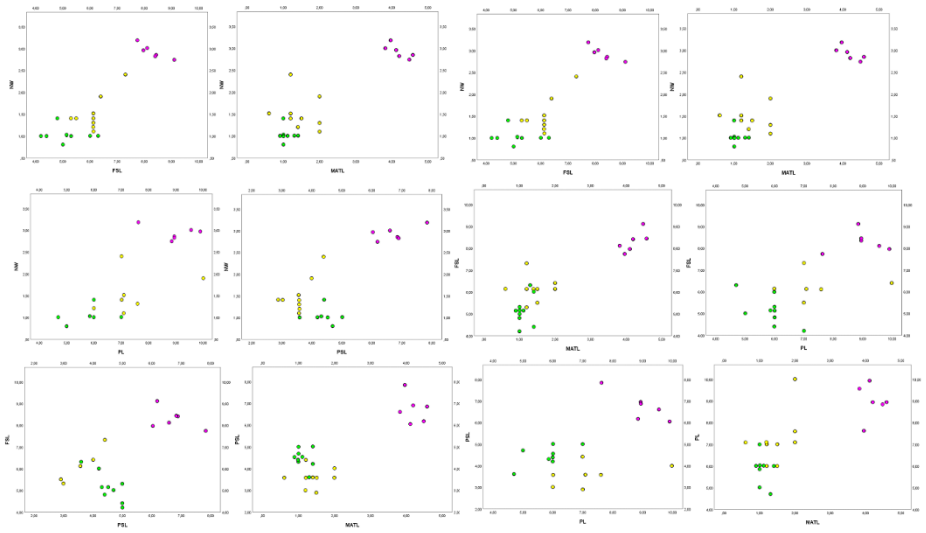

FIGURE 8. Bivariate and multivariate analyses among *D. anatolicus* (yellow circle), *D. laniger* (green circle), and *D. nitedula* (pink circle). A. Scatter plots of external variables for *D. anatolicus*, *D. laniger*, and *D. nitedula*. B. Scatter plots of skull and mandible variables (HFL, length of hindfoot; TL, length of tail; NW, nasal width; FSL, length of frontal suture; PSL, length of parietal suture; PL, palatal length; MATL, length of mandibular tooth row) for *D. anatolicus*, *D. laniger*, and *D. nitedula*

While the value ranges of external characters of 3 *Dryomys* species are as follows: (i) *D. anatolicus* TL 63.0–85.0 mm, HFL 16.0–21.0 mm (ii) D. laniger TL 25.0–82.0 mm, HFL 16.0–22.0 mm (iii) *D. nitedula* TL 95.0–117.0 mm, HFL 19.0–23.0 mm. The ranges of character values for the skull and mandible are as follows: (i) NW 1.1–2.4 mm, FSL 5.3–7.3 mm, PSL 2.9–4.4 mm, PL 6.0–10.0 mm, MATL 0.6–2.0 mm for *D. anatolicus* (ii) NW 0.8–1.4 mm, FSL 4.2–6.3 mm, PSL 3.6–5.0 mm, PL 4.7–7.0 mm, MATL 0.9–1.4 mm for *D. laniger* (iii) NW 2.7–3.2 mm, FSL 7.7–9.2 mm, PSL 6.0–7.8 mm, PL 7.6–9.9 mm, MATL 3.8–4.6 mm for *D. nitedula*.

3.2.2 Geometric morphometry

According to the centroid size analysis, it was determined that *D. anatolicus*, *D. laniger* and *D. nitedula* species were different from each other. When the average centroid size was examined, it was seen that *D. nitedula*, *D. laniger* and *D. anatolicus* had the largest skull and mandible, respectively (Figure 9). The ANOVA test results confirmed that there was a significant difference in the shape and dimensions of the dorsal, ventral and mandible of the skull among the three species groups ($p<0.0001$ and $p<0.05$) (Table 5). Differences in centroid sizes (skull and mandible) of *D. anatolicus*, *D. laniger* and *D. nitedula* were found (Table 5). It was revealed that *D. nitedula* was bigger than *D. anatolicus* and *D. laniger* on the other hand *D. anatlolicus* was found to be the smallest for both skull and mandible (Figure 9).

TABLE 5. ANOVA test results based on centroid size data of *Dryomys* species (Bold shows that Statistically Significant Difference)

	ANOVA	
	F Value	P Value
Dorsal Cranium	5.36	**0.0143**
Ventral Cranium	5.40	**0.0133**
Mandibles	30.43	**0.0001**

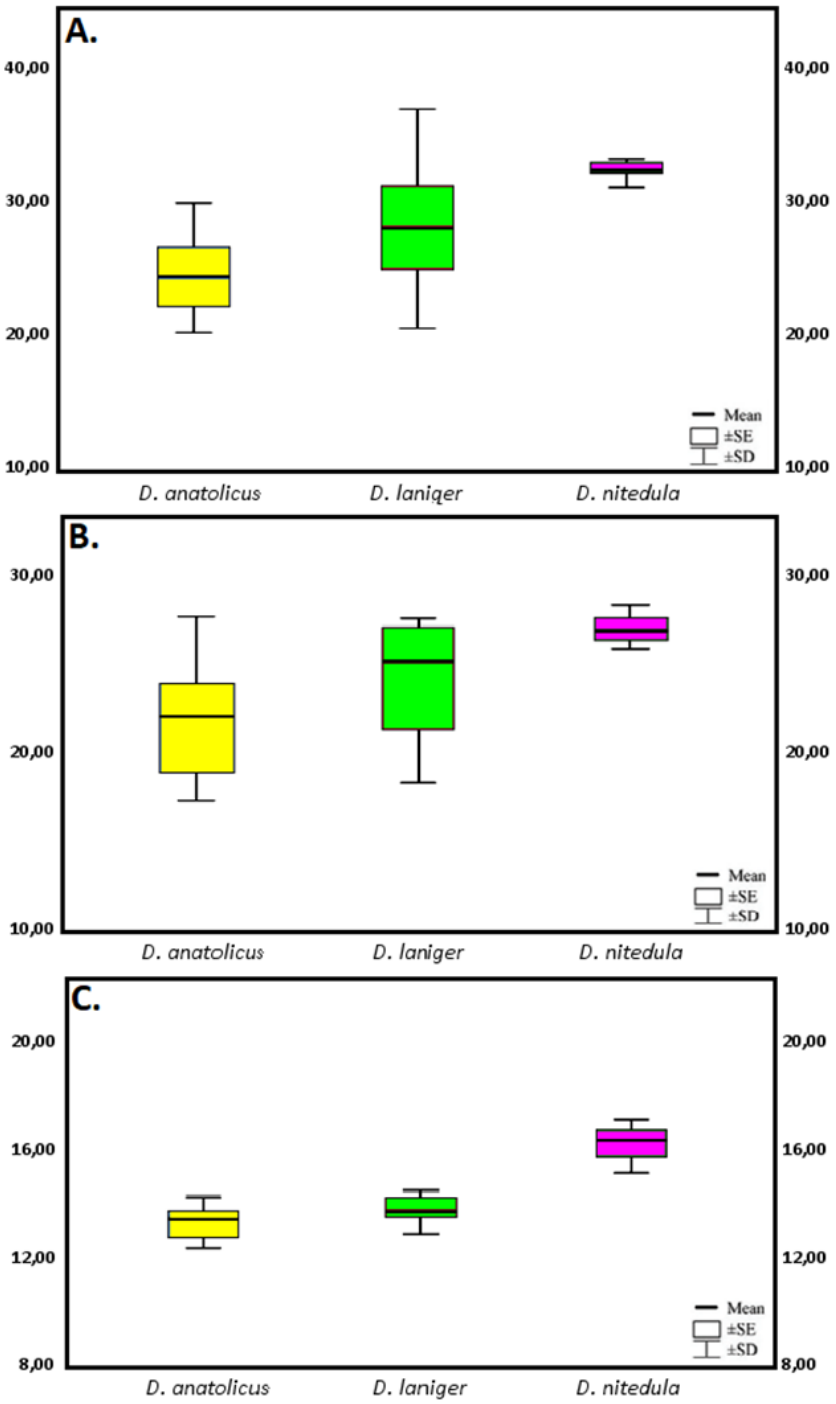

FIGURE 9. Box plot for dorsal, ventral cranium and mandible centroid sizes of *Dryomys* species (A: Dorsal Cranium; B: Ventral Cranium; C: Mandible)

According to the results of the PCA analysis, differences were observed in the shape area distributions of the dorsal, ventral and mandibular skulls of the specimens belonging to the *Dryomys* species. Accordingly, the first 6 components forming the dorsal part of the skull constituted 97% of the total variation. PC1 explained 53.69% and PC2 explained 21.24% of the total variation (Figure 10A). The first 8 components forming the ventral part of the skull constituted 97.47% of the total variation. PC1 explained 47.38% and PC2 explained 21.95% of the total variation (Figure 10B). When we look at the mandible, it was seen that the first 11 components constituted 96.65% of the total variation, while PC1 explained 38.10% and PC2 explained 19.10% of the total variation (Figure 10C).

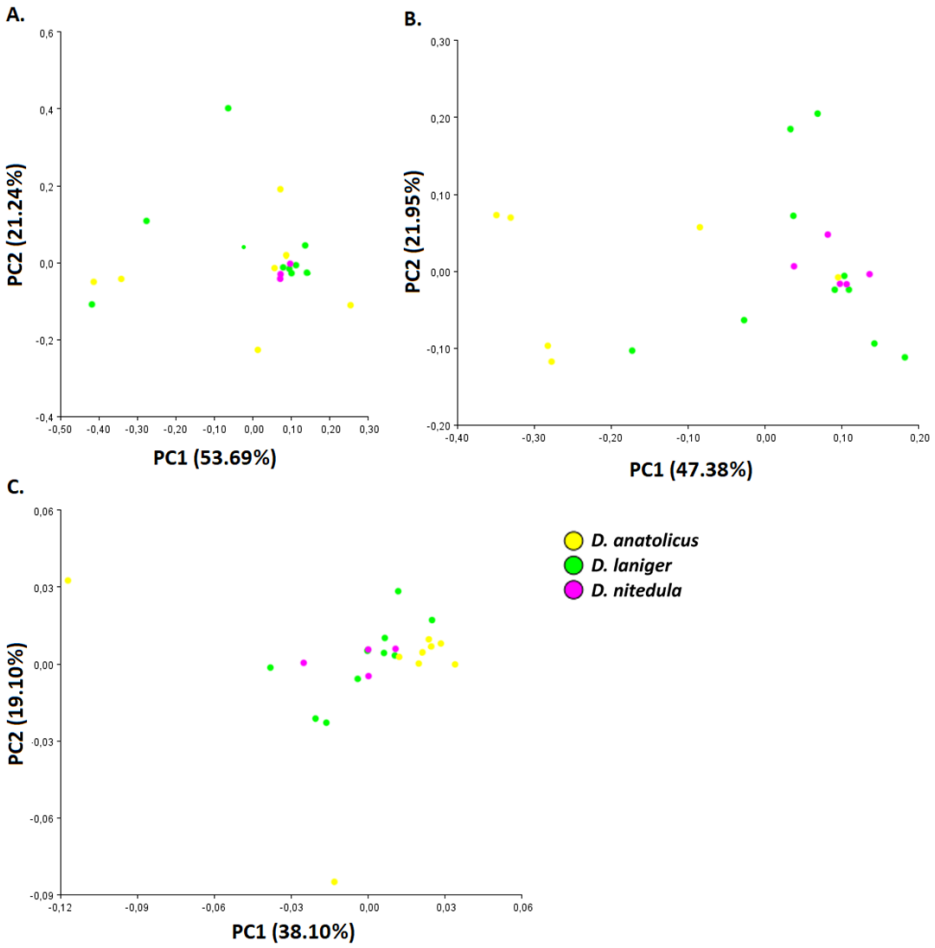

FIGURE 10. According to the Principal Component (PC), the scatter plots depict the dorsal cranium, ventral cranium, and mandibular characteristics in *Dryomys* species (A: dorsal part of the skull; B: ventral part of the skull; C: mandible)

Variations among species within the genus *Dryomys* (*D. anatolicus*, *D. laniger* and *D. nitedula*) were clearly explained by CVA analyses (Figure 11). The analysis performed for the dorsal aspect of the skull showed that *D. anatolicus* and *D. laniger* were grouped closer to each other in CV1 than *D. nitedula*, while in CV2, *D. anatolicus* and *D. nitedula* were grouped closer to each other than *D. laniger* (Figure 11A). Similarly, the analysis performed for the ventral aspect of the skull showed that *D. anatolicus* and *D. laniger* were grouped closer to each other in CV1 than *D. nitedula*, while in CV2, *D. laniger* and *D. nitedula* were grouped closer to each other than *D. anatolicus* (Figure 11B). Similarly, the analysis for the mandible showed that *D. anatolicus* and *D. nitedula* were grouped closer together in CV1 than in *D. laniger*, while in CV2, as in the ventral part of the skull, *D. laniger* and *D. nitedula* were grouped closer together than in *D. anatolicus* (Figure 11C). This analysis provides better resolution of intraspecific distinctions within the genus *Dryomys* than PCA.

The shape differences between the mentioned species were much better separated along the first axis of the scatter plot by CVA. In the analysis, CV1 for the dorsal part of the skull explained 93.16% of the total shape variation among the three species, CV1 for the ventral part of the skull explained 76.74%, and CV1 for the mandible explained 80.44%.

When the CVA results were examined, no statistically significant difference was found for Mahalanobis Distance for any of the species. According to the dorsal cranium data, the Mahalanobis and Procrustes distances between species groups and the permutation test differences based on these differences did not yield significant results. The ventral cranium data showed that *D. anatolicus* was significant in terms of Procrustes distances with *D. laniger* and *D. nitedula* and the permutation test differences based on these differences ($p<0.05$). Finally, when we examined the data belonging to the mandible, it was seen that *D. anatolicus* gave much more significant results than the ventral cranium in terms of Procrustes distances with *D. laniger* and *D. laniger* with *D. nitedula* and the permutation test differences based on these differences ($p<0.01$) (Table 6). When examined, it was shown that the CVA performed with both the data of the ventral cranium and the data of the mandible showed that all 3 species groups could be significantly and clearly separated from each other, but these 3 species groups did not show a significant difference even though they were clearly separated in the dorsal cranium (Figure 11).

TABLE 6. CVA results for dorsal, ventral cranium and mandible (Mah. Dist.: Mahalanobis Distance; Proc. Dist.: Procrustes Distance; Perm. P.: Permutation P Value), (Bold shows that Statistically Significant Difference)

Species Groups	*D. anatolicus*				*D. laniger*			
	Mah. Dist.	Perm. P.	Proc. Dist.	Perm. P.	Mah. Dist.	Perm. P.	Proc. Dist.	Perm. P.
Dorsal Cranium								
D. laniger	8.3734	0.1509	0.1407	0.3816	–	–	–	–
D. nitedula	25.6361	0.1918	0.1735	0.2820	19.9396	0.6661	0.1280	0.3437
Ventral Cranium								
D. laniger	4.9944	0.2710	0.2143	**0.0163**	–	–	–	–
D. nitedula	7.3040	0.1092	0.2551	**0.0145**	8.3879	0.2575	0.1059	0.1280
Mandible								
D. laniger	9.1697	0.4246	0.0428	**0.0044**	–	–	–	–
D. nitedula	8.8035	0.8010	0.0261	0.8452	13.9422	0.3971	0.039	0.0028

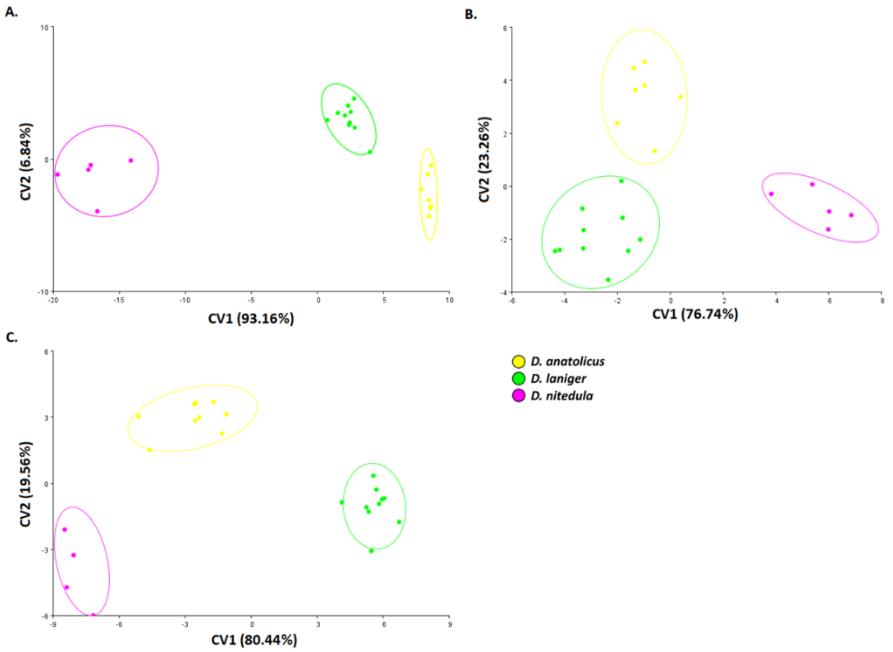

FIGURE 11. Scatter plots of results of Canonical Variate Analysis (CVA) in *Dryomys* species (A: Dorsal Cranium; B: Ventral Cranium; C: Mandible)

According to the Discriminant Function Analysis (DFA) results performed with skull and mandible data, it was observed that the correct separation of the groups from each other in the pairwise comparisons was quite high. This rate was 100% for the dorsal cranium, 100% for the ventral cranium and 97.4% for the mandible, respectively. In the pairwise grouping performed only for the mandible, 2 specimens belonging to *D. anatolicus* were grouped as *D. nitedula* (Figure 12). The average shape differences of the dorsal cranium, ventral cranium and mandible belonging to the species are shown in (Figure 13). The test results obtained during the Discriminant Function Analysis (DFA) showed that the shape differences of the dorsal cranium, ventral cranium and mandible belonging to the species groups were statistically significant (Table 7).

According to dorsal cranium data, *D. nitedula* differed from both *D. anatolicus* and *D. laniger* in terms of Permutation P Value test and this difference is statistically significant ($p<0.05$). Ventral cranium data showed that *D. anatolicus* differed from *D. laniger* and *D. nitedula* in terms of Procrustes Distance Value test and *D. nitedula* differed from *D. laniger* in terms of Permutation P Value test. These differences are $p<0.05$ and $p<0.01$ respectively and are statistically highly significant. Finally, when we examined the data belonging to the mandible, it was proven that *D. anatolicus* and *D. laniger* were different from each other in terms of the Permutation P Value test and *D. laniger* and *D. nitedula* in terms of both the Permutation P Value test and the Procrustes Distance Value test, and these differences were statistically significant ($p<0.01$, $p<0.05$) (Table 7).

TABLE 7. DFA results for dorsal, ventral cranium and mandible (T^2: T-square; Param. P.: Parametric P Values; Perm. P. (T^2): Permutation P Value; Perm. P. (Proc.): Procrustes Distance Value), (Bold shows that Statistically Significant Difference)

Species Groups	*D. anatolicus*				*D. laniger*			
	T^2	Param. P.	Perm. P. (T^2)	Perm. P. (Proc.)	T^2	Param. P.	Perm. P. (T^2)	Perm. P. (Proc.)
Dorsal Cranium								
D. laniger	147.3293	0.7645	0.0601	0.3833	–	–	–	–
D. nitedula	575.1780	0.3145	**0.0231**	0.2879	263.4833	0.5624	**0.0388**	0.3447
Ventral Cranium								
D. laniger	67.4610	0.8896	0.1069	**0.0143**	–	–	–	–
D. nitedula	35.6834	0.6710	0.5521	**0.0151**	136.2794	0.4704	**0.0088**	0.1302
Mandible								
D. laniger	238.0958	0.7141	0.1215	**0.0040**	–	–	–	–
D. nitedula	8.9454	0.9964	0.7884	0.8495	35.6136	0.9326	**0.0155**	**0.0027**

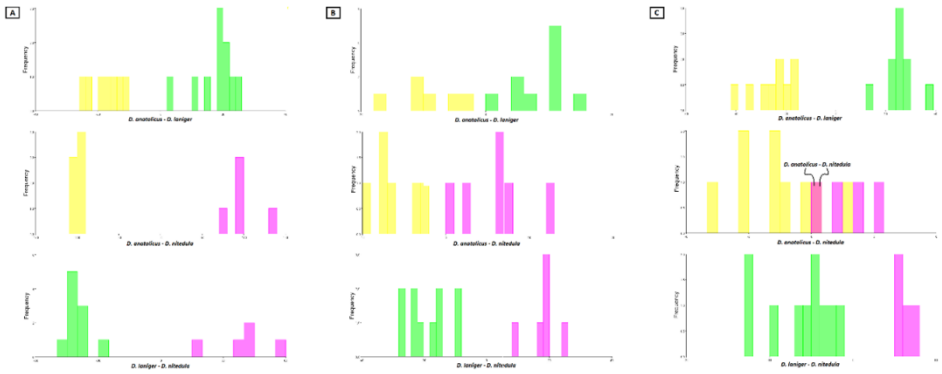

FIGURE 12. Scatter plots of result of Discriminant Function Analysis (DFA) in *Dryomys* species (A: Dorsal Cranium; B: Ventral Cranium; C: Mandible) (X-Axis: Discriminant Scores; Y-Axis: Frequency)

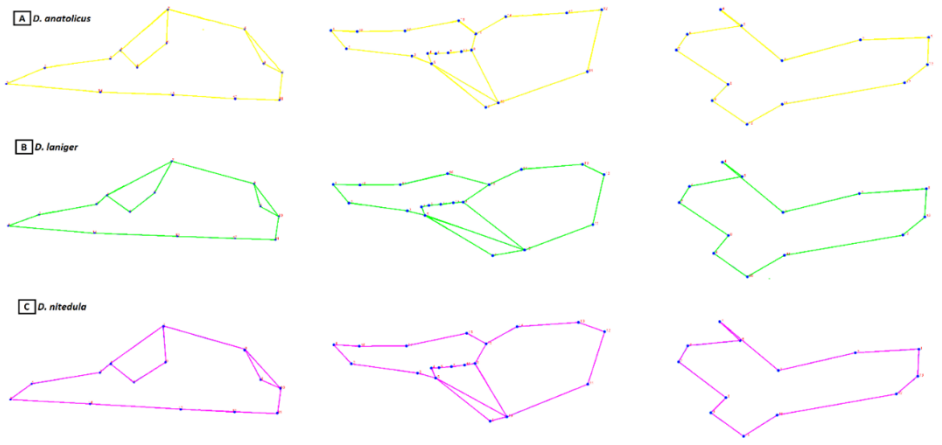

FIGURE 13. Discriminant Function Analysis (DFA) mean shape differences results for dorsal cranium, ventral cranium and mandible by respectively (A: *D. anatolicus*; B: *D. laniger*; C: *D. nitedula*)

3.3 Taxonomy

3.3.1 *Dryomys anatolicus* sp. nov.

urn:lsid:zoobank.org:pub:3AC02C5C-E8DA-47FA- 889B-73C9387EA937

3.3.2 Diagnosis and comparison

D. laniger has brownish dorsal fur on the contrary of *D. anatolicus* which has grey dorsal fur (Figure 14). According to morphological data from skull measurements (Table S3 and Figure 15) there are significant differences between two species. *D. laniger* has a larger skull than *D. anatolicus* (Figure 9). Dorsal, ventral and mandible of the skull are different (Table 5). Sexual dimorphism was not observed in our samples. Beside morphological differences there are also genetic differences between two species. Genetically distant clade in phylogenetic tree reconstructed with mtDNA (*CYTB*) and nuclear DNA (IRBP) marker. Kimura 2 parameter distance in *CYTB* between *Dryomys anatolicus* sp. nov. and *Dryomys laniger* is 7%.

3.3.3 Holotype

One adult female, the skin deposited at Zonguldak Bülent Ecevit University Molecular Systematic Laboratory (Sample no: 8715) (Figure 14). Skull, mandibular, and tissues preserved in RNA later solution.

3.3.4 Type locality and distribution

Type locality of the species is Eşekçayırı plateau, Ovacık, Tunceli, Turkey (39.420799 N, 39.240681 E, 1800 m). Another distribution record from Püren pass, Göksun, Kahramanmaraş, Turkey (37.931851 N, 36.503126 E, 1700 m).

3.3.5 Paratypes

Four females from the type locality (8712, 8713, 8714, and 8716) in addition to the type specimen (8715). One male (8682) and five females (8662, 8680, 8683, 8684, and 8685) from Püren pass, Göksun, Kahramanmaraş, Turkey.

3.3.6 Etymology

Since it is endemic to Anatolia, the name *D. anatolicus* was chosen.

3.3.7 Measurements of holotype

External characters and skull measurements (weight in g, other measurements in mm); Total length, 180; head and body, 103; Tail; 77, Hindfoot, 20; Ear; 15; Weight, 21; Zygomatic width, 12; Rostrum width, 3; Interorbital width, 2; Nasal Length, 7.3; Nasal width, 1.9; Frontal suture length, 6.4; Parietal suture length, 4; Brain capsule width, 9.7; Face area length, 12; Diestema length, 4.5; Palatal length, 10; Foramen incision length, 4.2; Upper tooth row length, 1.3; Rostrum height, 2; Lower tooth row length, 2; Mandible height, 4.4; Mandible length, 12.

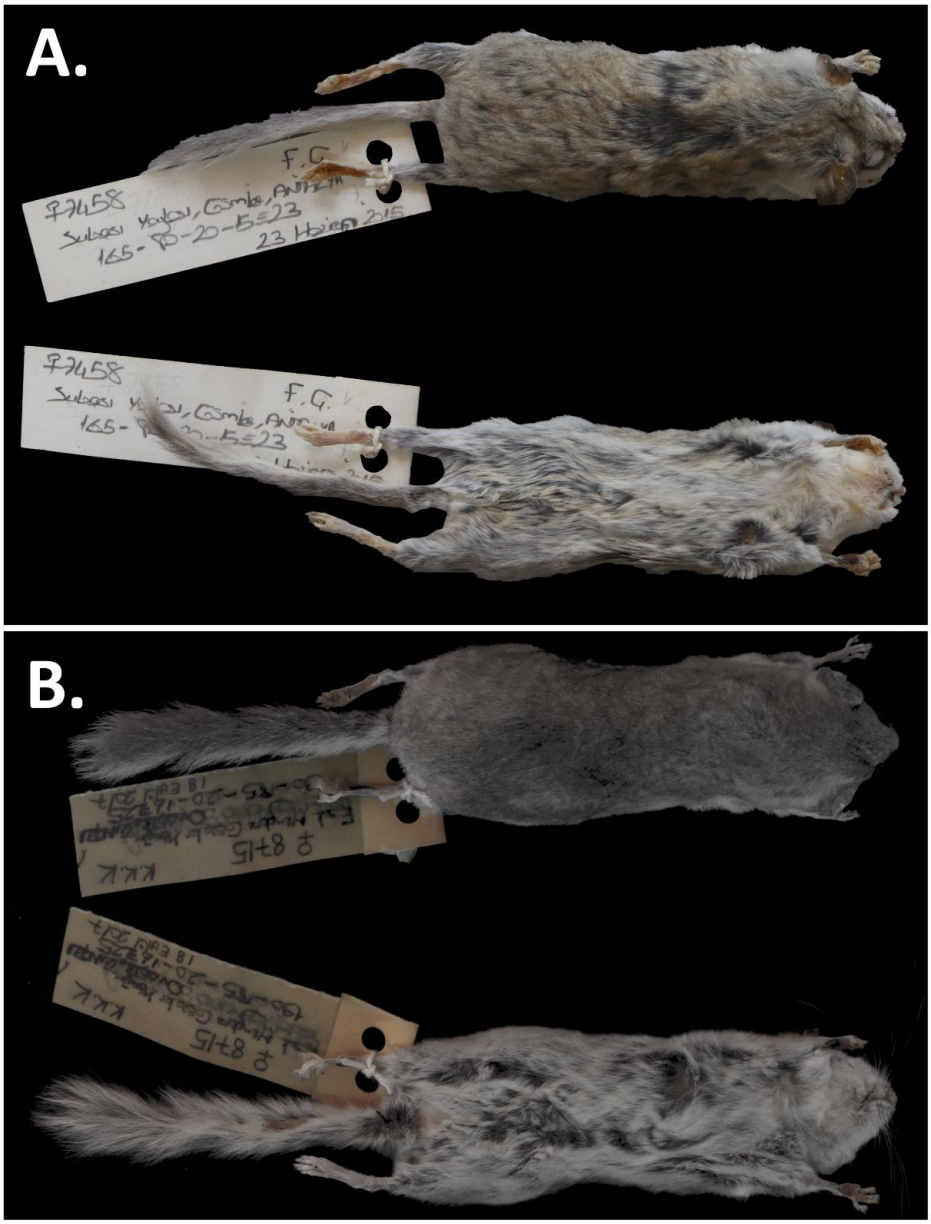

FIGURE 14. Skin of the *Dryomys laniger* (A) and *Dryomys anatolicus* sp. nov. (B)

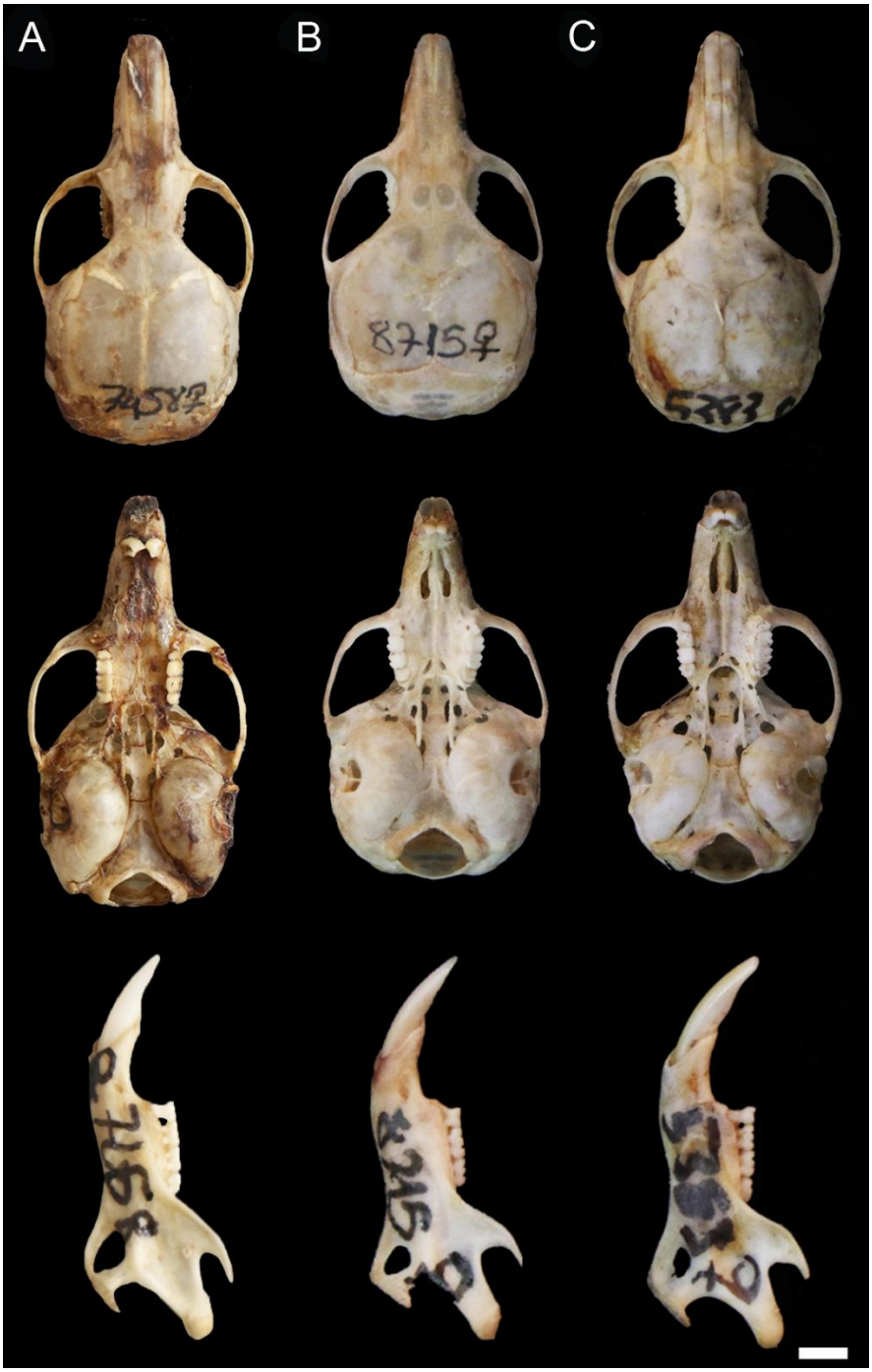

FIGURE 15. Skull and mandible of the *D. laniger* (A), type specimen (8715) of *Dryomys anatolicus* sp. nov. (B) and *D. nitedula* (C)

3.3.8 Habitat

Mountainous areas above 1700 m a.s.l. The species lives in rocky areas with sparse vegetation. The distribution area of the species is fragmented and apart from the type locality in Munzur Mountains (Figure 16), it has also been found in Püren Pass (province of Kahramanmaraş, Figure 17).

FIGURE 16. Habitat of *Dryomys anatolicus* type locality, Eşekçayırı Plateau (Munzur mountains), Ovacık, Tunceli

FIGURE 17. Habitat of *Dryomys anatolicus*, Püren pass (Armut mountains), Göksun, Kahramanmaraş

4. DISCUSSION

We presented the first results on the phylogeny, genetic diversity, and extended distribution records of *D. laniger*, a small rodent endemic to Anatolia with a highly fragmented distribution range. Besides resampling the four distribution areas that were previously identified, two new geographical locations have been recorded: the Çiçekliboyun plateau and the Subaşı plateau. Next, we found that the two populations with the easternmost distribution (Yellow clade) (Armut and Munzur mountains) possess sufficient genetic and morphological differences to warrant a new species status, *D. anatolicus sp. nov*. As alpine and montane species, *D. laniger* and *D. anatolicus sp. nov*. may have survived these areas through the Quaternary. It is likely that *D. laniger* and *D. anatolicus* had a wider distribution in the Quaternary than at present.

We can see a very deep divergence between *D. laniger* and *D. anatolicus* sp. nov. [43] The K2P distance of 7% in the full CYTB sequence is very high between these taxa, i.e. much higher than the threshold of 1,5 - 2,5% proposed by [44] for CYTB. Similar to Tobe and colleagues' work, [45] proposed a threshold of >2% to start considering the species rank. The same authors consider the genetic distance below 2% to indicate intraspecific variation: note that 2% is the level of divergence between clade 1 and clade 2 within the green clade of *D. laniger*. Beside CYTB, in the phylogenetic tree reconstructed with IRBP there is a clear seperation between *D. laniger* and *D. anatolicus* sp. nov. with a strong support (Figure 3). AMOVA also showed this deep divergence between *D. laniger* and *D. anatolicus* sp. nov. IRBP, as a nuclear gene, is particularly valuable in phylogenetic studies of mammals and other vertebrates because it provides complementary insights to mitochondrial markers like CYTB, which can sometimes reflect only maternal inheritance patterns [46–48].

According to the divergence between ancestors of *D. laniger*/*D. anatolicus* sp. nov. clade and *D. nitedula* which occurred ~25 mya, the two species separated from each other in the Oligocene. During the Eocene/Oligocene transition an extinction/immigration event occurred called “grande coupure” about 33 mya. During that time dormice survived and they were also very successful [49]. They continued to diversify throughout the Oligocene and early Miocene [50]. Our hypothesis is that during the Oligocene because of the uplift of Anatolia, ancestors of *D. laniger* and *D. anatolicus* separated from *D. nitedula* and became isolated at the high altitudes in Anatolia [51]. When the uplift event gradually occurred some populations could adapt and prevail through these topographic changes [16]. We think that the ancestors of *D. laniger* and *D. anatolicus* may have adapted to the alpine environments and speciation events occurred allopatrically between these two species. This hypothesis is consistent with the idea that Spitzenberger presented in 1976. According to their opinion, the divergence of *D. laniger* and *D. nitedula* dates back to the late Oligocene. They also proposed that these two species allopatrically diverged from each other.

Two endemic species from Anatolia, *D. laniger* and *D. anatolicus*, diverged from each other ~6 mya. Our hypothesis on the separation event of the species is that *D. anatolicus* migrated to the east first to extend its distribution range. Then when the Messinian dry climate conditions occur in the whole Mediterranean, two populations on the Anatolian Diagonal mountain system (Armut mountains and Munzur mountains) were isolated from *D. laniger* populations which are distributed in the Taurus mountains. At the end of the Messinian epoch, Taurus mountain populations and populations on the Anatolian Diagonal separated from each other at the species level. This event is a good example of peripatric speciation. Ancestral populations harbor more genetic diversity than later immigrants to the new areas [52–54]. In our case, genetic diversity also showed that *D. laniger* is the origin of the *D. anatolicus* because *D. laniger* is genetically more diverse and also even clades of *D. laniger*'s genetic diversity is greater than *D. anatolicus*. Mismatch distribution analyses also showed that both species had several population expansion events in the past.

The two clades within the green clade of *D. laniger* (clade 1 and clade 2) diverge from each other by 1.85 mya. It can be inferred that the separation of these two clades is affected by the climate. In Messinian, *D. laniger* became a separate species, and clades of these species survived on the mountaintops. As an alpine species, *D. laniger* couldn't migrate downhill from the mountaintops in Messinian dry climate. Thus two clades couldn't meet again in Quaternary although ice ages started which have better climatic conditions for an alpine species. The genetic difference between these two clades is 1,9% according to K2P distance. Tobe et al. 2010 proposed a threshold (K2P 1,5%) to separate the species. Our value is higher than this value but we didn't see any difference between morphology. Thinking about the future climate, these two clades are going to stay isolated.

Dryomys laniger currently has a DD (Data Deficient) status according to the IUCN classification, due to very few and sporadic distribution records and the lack of studies on its general biology. As a new species, obviously *D. anatolicus* has no information in the IUCN Red List of Threatened Species. Our observations of the landscapes where both species are found suggest that human impact, especially various mining activities in the Anatolian mountains, may adversely affect the extant populations. In addition, since *D. laniger* and *D. anatolicus* prefer a very specific habitat (steep rock faces), habitat destruction in these areas can have irreversible consequences. Subject to genetic bottleneck and increased chance of extinction, the current populations seem to be poorly equipped facing the threat of additional habitat destruction and the warming climate in the mountainous areas. Active conservation programs are urgently required for all known populations in the Taurus mountains and the Anatolian diagonal. Efforts to discover additional populations in the Anatolian mountains are equally important.

Finally, to better understand the evolutionary histories of two endemic dormouse species, genomic data would be best to resolve the complex taxonomy of this group. The sample sizes for future studies should be increased. We must

therefore reiterate that better genotyping is required to reconstruct the full evolutionary history of this species, beyond that of just mitochondrial lineages demonstrated in our study.

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Author Contribution Statements Ferhat Matur and Mustafa Sözen obtained funding and Mustafa Sözen supervised the study. Ortaç Çetintaş, Faruk Çolak, Kürşat Kenan Kalkan, Ferhat Matur and Mustafa Sözen took part in fieldwork and collected samples. Kürşat Kenan Kalkan analyzed the morphological data. Ortaç Çetintaş and Sercan Irmak performed lab work and analyzed the data. Ortaç Çetintaş designed the study and wrote the paper. All authors approved the final version of the manuscript.

Declaration of Competing Interests The authors declare no conflict of interest.

Ethical Statement The procedure was approved by Zonguldak Bülent Ecevit University Animal Experiments Ethics Committee (permit no. 91330202-10).

Use of Artificial Intelligence No artificial intelligence-based tools or applications were used in the preparation of this study. The entire content of the study was produced by the author(s) in accordance with scientific research methods and academic ethical principles.

Data availability The voucher specimens were deposited in the Molecular Systematics Laboratory in Zonguldak Bülent Ecevit University.

Appendix A. Supplementary data

Supplementary Table S1

Supplementary Table S2

Supplementary Table S3

Supplementary Table S4

Supplementary Table S5

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