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## Occlusal surface variations in genetically-identified specimens of the genus *Apodemus* (Mammalia: Rodentia) distributed in the Northern Anatolia region and three Turkish islands: Gökçeada, Marmara Island, and Bozcaada

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**Abstract:** A total of 134 *Apodemus* samples, whose genetic diagnoses had been previously conducted, were morphologically examined from 39 localities in Northern Anatolia, Thrace, Gökçeada, Bozcaada, and Marmara Island. The variation boundaries of dental variations in the distribution areas of five *Apodemus* species (*Apodemus flavicollis*, *Apodemus witherbyi*, *Apodemus sylvaticus*, *Apodemus uralensis*, *Apodemus mystacinus*) included in the research were determined. The defining morphological characters of *Apodemus* species, which have a complex taxonomic status, and their variations according to regions were identified using samples that had undergone genetic diagnoses. It was determined whether geographical barriers such as the Marmara Sea, the Bosphorus and the Dardanelles, Melet River, Çoruh River and Kızılırmak separate populations of species from each other. It was found that the Kızılırmak likely caused a divergence in *A. mystacinus* samples, the Bosphorus and the Dardanelles likely caused a divergence in *A. flavicollis* species. However, it was not determined that the Melet River and Çoruh River caused a divergence within the species. Similarities and differences between island populations and mainland populations were identified in *Apodemus* species with distribution on islands. The differences observed in the Eastern-Western transition in Northern Anatolia were determined within the species and associated with habitats.

**Key words:** Turkish islands, *Apodemus*, occlusal surface, Türkiye

### 1. Introduction

Rodents are grouped into the order Rodentia. The genus *Apodemus* belongs to the family Muridae and the subfamily Murinae within the order Rodentia (Filippucci et al., 2002; Wilson and Reeder, 2005). Species of the genus *Apodemus* Kaup, 1826 are widespread rodents inhabiting forest, steppe, and rocky areas in the temperate zone of the Palearctic region (Filippucci et al., 2002; Wilson and Reeder, 2005). Unlike the *Mus* and *Rattus* genera, which have undergone artificial expansions due to human distribution, the *Apodemus* genus, belonging to this subfamily, has a natural distribution and represents one of the ancestral members (Ellerman, 1941). Although the described species are divided into subgenera *Apodemus*, *Sylvaemus*, *Alsomys*, and *Karstomys*, a consensus has not been reached.

The six *Apodemus* species occurring in Türkiye (*A. mystacinus*, *A. flavicollis*, *A. sylvaticus*, *A. agrarius*, *A. witherbyi*, and *A. uralensis*) have been extensively studied morphologically, morphometrically, and molecularly both in Türkiye and worldwide (Frynta et al., 2001; Çolak et al., 2005; Renaud, 2005; Frynta et al., 2006; Çolak et al., 2007; Javidkar et al., 2007; Siahsarvie and Darvish, 2008).

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Based on the literature provided above, it is challenging to distinguish between *Apodemus* species. One reason for this difficulty may be the different morphological responses exhibited by individuals of the same species in similar habitats or by individuals of the same species in different habitats. Morphology is an essential component of classification and taxonomy, preceding molecular studies. Therefore, it is crucial to identify distinguishing characters in the morphological analysis of genetically closely related specimens and to examine their presence in individuals from different habitats to determine species and subspecies. Phenotypic differentiation observed despite genetic homogeneity may be attributed to climatic, topographic, anthropogenic, and ecological factors influencing intraspecific biogeographic changes.

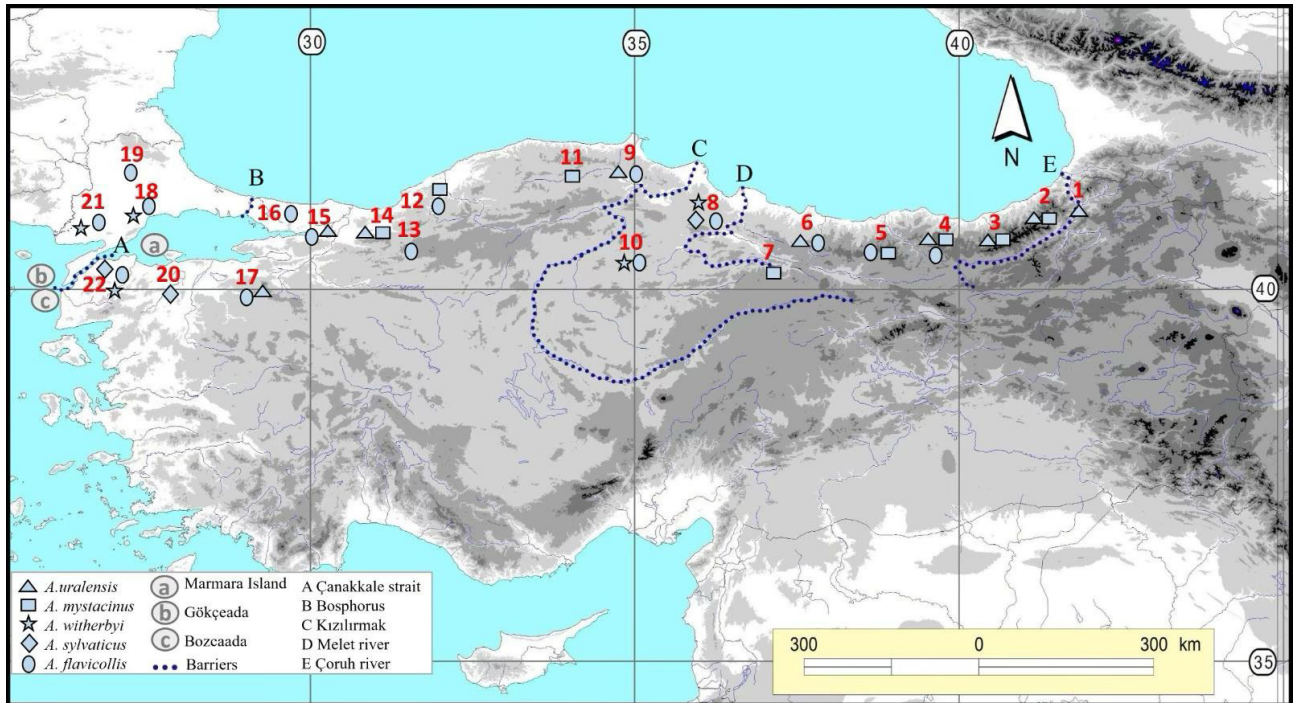
Molar teeth are often used as an important research resource in morphology, as they reflect the evolutionary adaptation of individuals in a population based on diet (Ungar, 2015). The samples in this study also include island populations in the Marmara and Aegean Seas. Islands hold significant importance in evolutionary and ecological studies. Over the past 30 years, investigations focused

on island biology have demonstrated the presumed significance of islands in revealing ecological relationships among organisms (Lack, 1976; Williamson, 1981). Rodent populations isolated on islands often exhibit systematic differences in demography, reproduction, behavior, and morphology compared to mainland populations (Chevret et al., 2021), and these differences are referred to as the island syndrome (Adler and Levins, 1994). Islands are of great importance for studying the acquisition or randomly selected morphological characters by populations due to the disruption of mainland connections and the cessation of gene flow and bottleneck effect. Some of the *Apodemus* species inhabit the islands in the Marmara and Aegean Seas. In this study, populations of *A. sylvaticus* and *A. witherbyi* collected from Marmara Island (Figure 1a), Gökçeada (Figure 1b), Bozcaada (Figure 1c), and whose genetic relatedness has been determined, were investigated. It is important to examine the degree of differentiation among populations of these species due to isolation from the mainland and to determine the relationship similar between island populations and mainland populations (García-Rodríguez et al., 2018), as well as the connections brought about by land bridges due to the increased glaciers and decreased sea levels during the Pleistocene period (Michaux et al., 2005).

Due to the lack of well-defined variation limits for morphological differentiating characters of *Apodemus* species that share similar habitats (Mikulova and Frynta, 2001) in Türkiye, confusion arises in species identification. In this regard, it is easier to determine the variation limits of differentiating morphological characters in specimens of species with known genetic relatedness. Therefore, samples of *A. flavicollis*, *A. sylvaticus*, *A. mystacinus*, *A. uralensis*, and *A. witherbyi*, whose phylogenetic relatedness has been determined through mtDNA cytb and mtDNA control region analyses (Selvi, 2019) were used in this study. The aim was to determine the morphological variations in the occlusal surface within the distribution range of these species. Understanding the reasons behind intra-specific and interspecific geographic variations, based on paleogeographic factors, and elucidating the isolation effects of geographical barriers such as the Marmara Sea, the Bosphorus and the Dardanelles, the Melet River, the Çoruh River, and the Kızılırmak, are important (Figure 1).

## 2. Materials and methods

In this study, a total of 134 *Apodemus* samples, were collected from 39 different locations and stored at Ankara University Mammalian Research Collection (AUMAC). In the planned fieldwork (Figure 1), samples were collected



**Figure 1.** Map of the locations where the samples were collected and main locations (modified from Çolak et al., 2013) A: The Dardanelles, B: The Bosphorus, C: Kızılırmak, D: Melet River, E: Çoruh River, a: Marmara Adası, b: Gökçeada, c: Bozcaada, 1-Ardahan, 2-Artvin, 3-Rize, 4-Trabzon, 5-Giresun, 6-Ordu, 7-Tokat, 8-Samsun, 9-Sinop, 10-Çorum, 11-Kastamonu, 12-Zonguldak, 13-Bolu, 14-Düzce, 15-Kocaeli, 16-İstanbul, 17-Bursa, 18-Tekirdağ, 19-Kırklareli, 20-Balıkesir, 21-Edirne, 22-Çanakkale.

using trapping devices and brought to the Molecular Systematics Laboratory of the Department of Biology, Ankara University. Measurements of total length, tail length, ear length, and hindfoot length were taken for each specimen. Subsequently, tissue samples were obtained from the weighed specimens and preserved for museum purposes. The collected skulls were labeled and boiled in 10% ammonia at 70 °C for 15 min (with frequent monitoring) and then cleaned using forceps, scalpel, etc. The cleaned skulls were examined under a microscope, and dental photographs were taken. The locations and variations of cusps on the upper teeth were examined (Figure 2a). The number and size of cingulum structures on the labial side in Lower Molar 1 (LM1) and Lower Molar 2 (LM2), the size of the talonid basin structure, whether there is a connection between labial and lingual anteroconids, the presence and size of the central distoconid structure, the presence of cingulum structure on the lingual side, and the shape of the anteroconid complex structure have been investigated (Figure 2b). Variations such as bis structure, spur structure, connections between cusps, shape of t7 cusp, and presence of t12 were detected in the Upper Molar 1 (UM1), Upper Molar 2 (UM2), and Upper Molar 3 (UM3) (Figure 3). Then, the location of the variations on each tooth was determined. For each sample, each character was examined, and percentages were calculated for the data prepared in tables. The study focused on the left teeth both of lower and upper. In the study, age determinations were made based on the condition of wear on the third upper molar tooth and the fusion state of the sutura coronalis. Both male and female individuals were evaluated, and only intact characters

were examined. The samples used in the study, along with their locations, are provided in the following tables (see Appendix). The samples used in the study are preserved in the Department of Biology A.U. Mammalian Research Collection (AUMAC). The obtained 1 and 0 data were analyzed in PAST 4.15 software with cluster analysis.

### 3. Results

#### 3.1 Upper molars and lower molars occlusal surface variations of *Apodemus flavicollis* (Melchior 1834)

A total of 44 genetically-diagnosed samples of *A. flavicollis* were examined. Anatolian and Thracian samples were compared in terms of determined characters and molar tooth morphologies. The frequencies of character occurrence were calculated as percentages within the two separate populations. It was observed that the samples from Anatolia and Thrace differed in terms of the characters D1, D4, D8, D9, and D13 (Table 1). The number of cingula is usually three or more (Figure 4.1a) in LM1. In less than 12% of the samples, one or two cingula were observed. The tma structure is generally of the same size and relatively small, connected to the labial and lingual anteroconids (Figure 4.1b). The central distoconids in *A. flavicollis* samples are considerably reduced and often almost absent (Figure 4.1c). No lingual projection was observed in any of the samples. The anteroconid complex is typically thick and, in most samples, the lingual anteroconid projects upwards from the labial side (Figure 4.1d). Extra cingula are generally not observed in LM2 (Figure 4.1e), and in very few cases, one or two cingula were found on the labial side. The labial anteroconid shows no variation, remaining the same size and in the same position in nearly all samples.

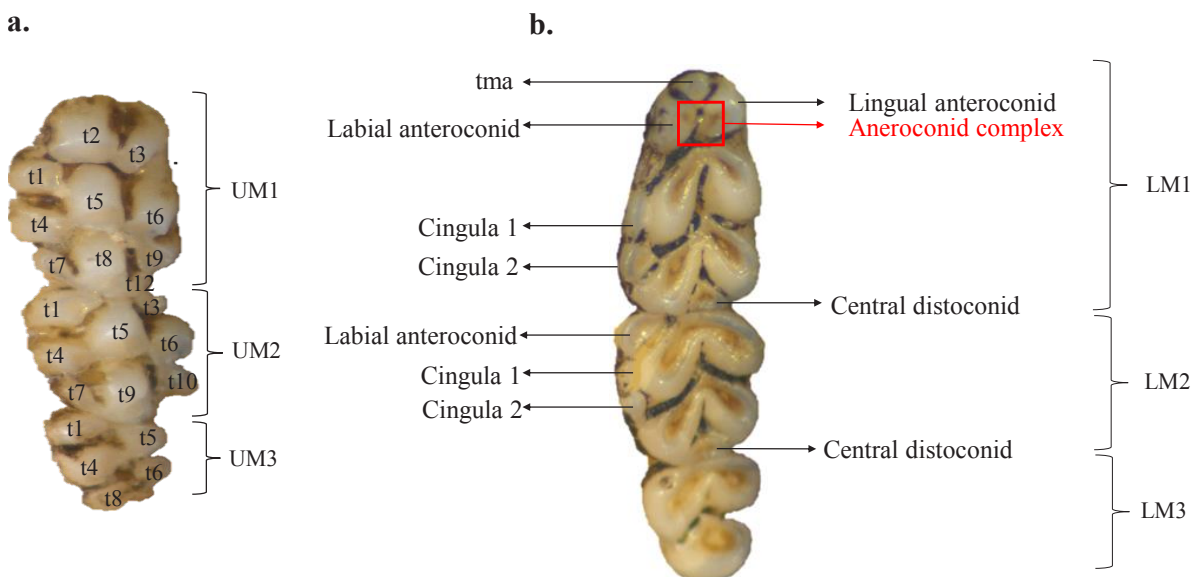
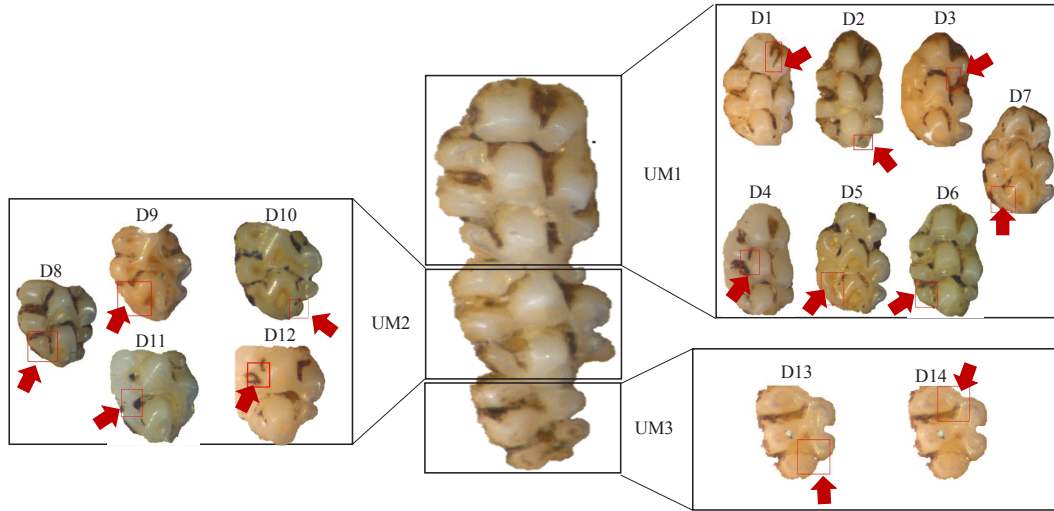


Figure 2. Nomenclature of upper (a) and lower (b) teeth (Zykov and Izvarin 2020).



**Figure 3.** The variations observed in the left upper teeth and their locations. D1: Presence of a bis structure immediately adjacent to the t2 cusp in UM1, D2: Presence of the t12 cusp in UM1, D3: Presence of a spur structure extending posteriorly from the t3 cusp in UM1 but not merging with the t5 cusp, D4: Existence of a bridge between the t1 cusp and t5 cusp in UM1, D5: Connection through a bridge between the t4 cusp and t7 cusp in UM1, D6: Structural swelling and island-like condition of the t7 cusp in UM1, D7: Structural line-like condition of the t7 cusp in UM1, D8: Structural swelling and island-like condition of the t7 cusp in UM2, D9: Line-like structural condition of t7 in UM2, D10: Presence or absence of the t12 cusp in UM2, D11: Presence of a bridge-like structure between the t1 cusp and t5 cusp in UM2, D12: Presence of a bridge between the t4 cusp and t7 cusp in UM2, D13: Existence of a bridge structure between the t1 cusp and t5 cusp in UM3, D14: Presence of a connection between the t6 cusp and t8 cusp in UM3.

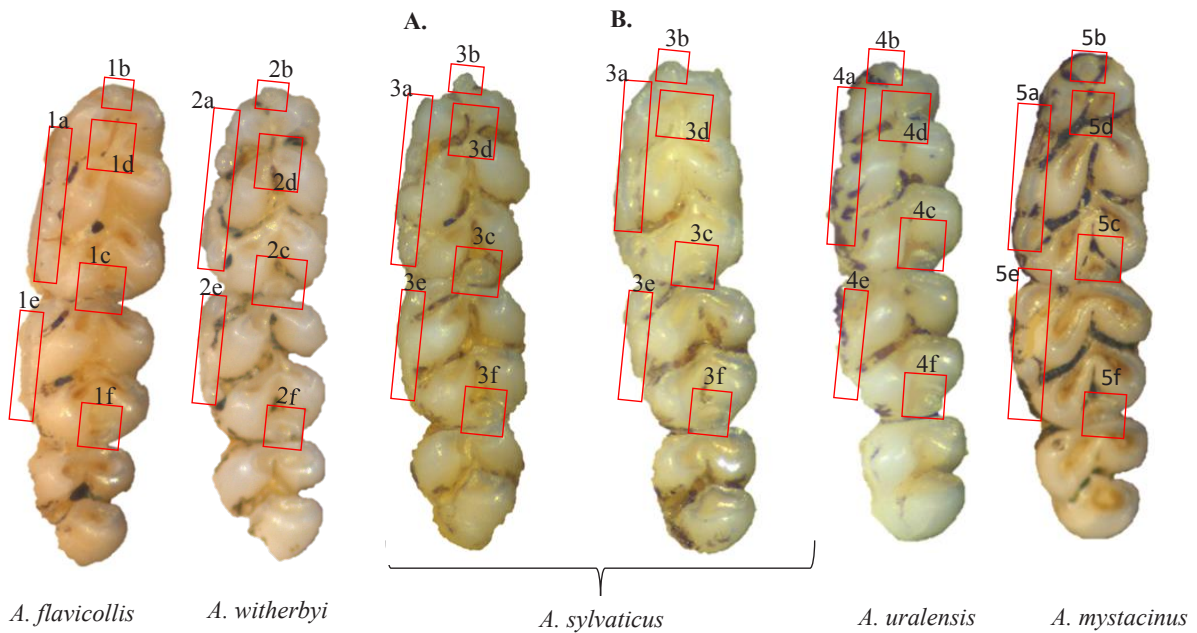
**Table 1.** A table constructed based on the frequencies of observed variations within the sample groups. AfAna: *A. flavicollis* Anatolian samples, AfThr: *A. flavicollis* Thrace samples, AwAna: *A. witherbyi* Anatolian samples, AwThr: *A. witherbyi* Thrace samples, AwBA: *A. witherbyi* Bozcaada samples, AsAna: *A. sylvaticus* Anatolian samples, AsGA: *A. sylvaticus* Gökçeada samples, AsMI: *A. sylvaticus* Marmara Island samples, AuEB: *A. uralensis* Eastern Black Sea samples, AuWB: *A. uralensis* Western Black Sea samples, AmEB: *A. mystacinus* Eastern Black Sea, AmWB: *A. mystacinus* Western Black Sea samples.

Regions	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14
AfAna	9%	66%	85%	33%	19%	42%	57%	31%	68%	%0%	0%	25%	31%	62%
AfThr	60%	53%	93%	80%	26%	46%	53%	53%	46%	%0%	6%	26%	66%	33%
AwAna	0%	75%	100%	75%	25%	25%	75%	50%	50%	%0%	50%	75%	0%	50%
AwThr	0%	62%	50%	75%	62%	12%	87%	25%	75%	0%	12%	12%	12%	50%
AwBA	0%	40%	100%	100%	80%	60%	40%	40%	60%	%0%	60%	80%	0%	100%
AsAna	0%	33%	66%	66%	33%	33%	66%	33%	66%	%0%	0%	66%	0%	0%
AsGA	100%	50%	100%	0%	100%	0%	100%	0%	100%	%0%	50%	100%	100%	100%
AsMI	100%	100%	0%	0%	50%	50%	50%	50%	50%	%0%	0%	50%	50%	0%
AuEB	0%	0%	22%	16%	11%	22%	44%	0%	100%	%0%	0%	0%	12%	50%
AuWB	14%	14%	57%	28%	14%	28%	71%	0%	100%	%0%	0%	16%	0%	16%
AmEB	0%	85%	100%	0%	30%	80%	20%	76%	23%	%100%	0%	17%	6%	31%
AmWB	0%	100%	60%	0%	0%	100%	0%	60%	40%	%100%	0%	0%	0%	40%

However, central distoconids are reduced and nearly absent of *A. flavicollis* samples (Figure 4.1f). No significant differences were detected in the structure of lower molars in *A. flavicollis* samples based on regional variations such as Anatolian-Tracian or Eastern-Western.

### 3.2 Upper molars and lower molars occlusal surface variations of *Apodemus witherbyi* (Thomas 1902)

A total of 19 genetically-diagnosed samples of *A. witherbyi* were examined, including specimens from Anatolia, Thrace, and Bozcaada. Specimens from Bozcaada



**Figure 4.** The intra- and interspecies schematic diagram of left lower dental variations. Diagram A: refers to the island population of *A. sylvaticus*, while B: refers to the mainland population of *A. sylvaticus*. Numbers represent species; 1: *A. flavicollis*, 2: *A. witherbyi*, 3: *A. sylvaticus*, 4: *A. uralensis*, 5: *A. mystacinus*. Lowercase letters have been selected as variation characteristics; a: number of cingula in LM1, b: tma in LM1, c: central distoconid in LM1, d: aneroconid complex in LM1, e: number of cingula in LM2, f: central distoconid in LM2.

exhibited differences from both Anatolian and specimens from Thrace in some characters (D2, D6, D7, D14) while showing similarities to specimens from Thrace based on D5 and D9 (Table 1). In most samples, the number of cingula in LM1 is three or more (Figure 4.2a). The tma structure is generally of the same size and relatively small, connected to the labial and lingual anteroconids (Figure 4.2b). The central distoconids in *A. witherbyi* are relatively more developed and larger compared to *A. flavicollis* (Figure 4.2c). No lingual projection was observed in any of the samples. The aneroconid complex is usually thick, and in most samples, the lingual and labial anteroconids converge in the middle without any inward notching (Figure 4.2d). In LM2, extra cingula are often observed, and there may be two or three of them (Figure 4.2e). The labial anteconid shows no variation, remaining the same size and in the same position in nearly all samples. However, central distoconids are well-developed and larger (Figure 4.2f). When examining the lower teeth in *A. witherbyi* samples, no variation based on location, such as Anatolia-Thrace or Island-Mainland, was detected.

### 3.3 Upper molars and lower molars occlusal surface variations of *Apodemus sylvaticus* Linnaeus (1758)

A total of 7 genetically-diagnosed samples of *A. sylvaticus* were examined, including specimens from Gökçeada, Marmara Island, and the mainland. Morphological differences were observed in the variations D1, D4, and

D13 between the island and mainland samples. Specimens from Marmara Island showed similarity to specimens from mainland samples in D6, while the specimens from Gökçeada exhibited similarity to the mainland in D3 (Table 1). In LM1, the number of cingula is mostly three or more in the samples (Figure 4.A.3a). The tma structure is generally of the same size and relatively small, connected to the labial and lingual anteroconids (Figure 4.A.3b). The central distoconids in samples from island populations are relatively more developed and larger (Figure 4. A.3c), while in samples from Anatolia, they are reduced (Figure 4.B.3c). No lingual projection was observed in any of the samples. The aneroconid complex is generally thick. In most samples, the lingual anteroconid projects upwards from the labial side (Figure 4.3d). Extra cingula are generally not observed in LM2 (Figure 4.3e). The labial anteconid shows no variation, remaining the same size and in the same position in nearly all samples. However, the central distoconids are well-developed in island samples (Figure 4.A.3f.), while in Anatolian samples, they are reduced (Figure 4.B.3f). This information provides important insights into the dental morphology and variation among different populations of *A. sylvaticus*. This result should be further evaluated with more samples.

### 3.4 Upper molars and lower molars occlusal surface variations of *Apodemus uralensis* (Pallas 1811)

A total of 27 genetically-diagnosed samples of *A. uralensis* were examined. The samples were categorized as the

Western Black Sea Region (between Bursa and Ordu, excluding Ordu) and the Eastern Black Sea Region (between Ordu and Ardahan, including Ordu). No significant differences were observed between the research groups. Additionally, minor variations were detected among the samples (Table 1). Also, it was determined that the Melet River, which is among the sample groups, did not have a differentiating effect. The number of cingula is generally three or more (Figure 4.4a) in LM1. The tma structure is generally of the same size and relatively small, connected to the labial and lingual anteroconids (Figure 4.4b). The central distoconids in *A. uralensis* specimens are relatively well-developed (Figure 4.4c). In most samples, the lingual and labial anteroconids unite at the center, and no inward projection is observed. The anteroconid complex is generally thick. Extra cingula are generally not observed in LM2 (Figure 4.4d). No lingual projection was observed in any of the samples (Figure 4.4e). The labial anteroconid shows no variation, remaining the same size and in the same position in most of the samples. However, the central distoconids are relatively well-developed (Figure 4.4f). When examining the lower teeth of *A. uralensis* specimens, no variation associated with locations such as the Western Black Sea and Eastern Black Sea was detected. Also, no effect of the Melet River was found.

### 3.5 Upper molars and lower molars occlusal surface variations of *Apodemus mystacinus* (Danford and Alston 1877)

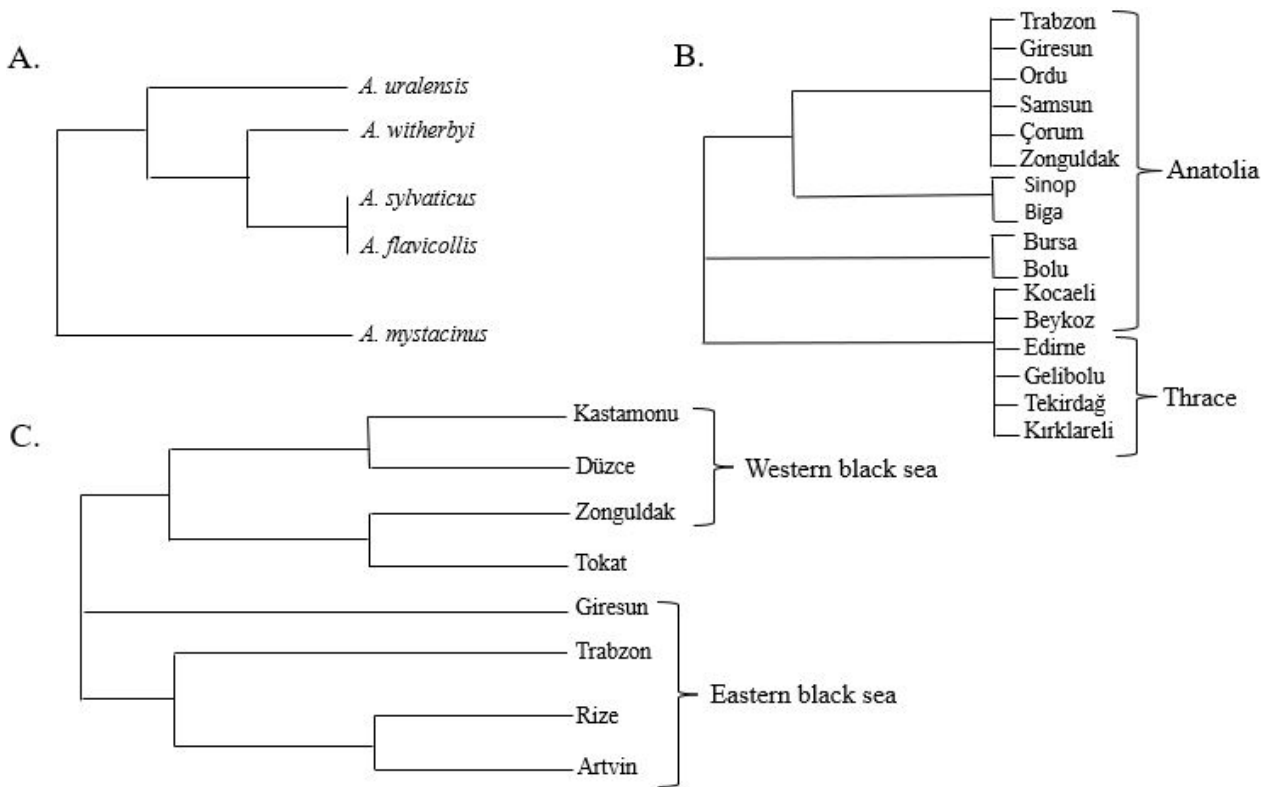
A total of 37 genetically-diagnosed samples of *A. mystacinus* were examined. Specimens were grouped into two groups, Western and Eastern Black Sea Regions, and the barrier effect of the Kızılırmak, which lies between the sample groups, was investigated. Morphological differences between the western and eastern sides of the Kızılırmak were identified in some characters, D3, D5, D6, D7, D9, and D12 (Table 1). The number of cingula is generally three or more (Figure 4.5a) in LM1. The tma structure is usually of the same size and relatively small (Figure 4.5b). The connection between labial and lingual anteroconids is absent in 39% of the samples. Central distoconids are relatively well-developed in *A. mystacinus* specimens (Figure 4.5c). Lingual projection is not observed in any of the samples. The anteroconid complex is generally thick in structure, and in most samples, the lingual anteroconid protrudes upward from the labial side (Figure 4.5d). Cingula are generally observed, and their number can reach up to three (Figure 4.5e) in LM2. There is no exceptional condition in the labial anteroconid; it remains consistent in size and position in almost all samples. Central distoconids are relatively well-developed (Figure 4.5f) When examining the lower teeth of *A. mystacinus* specimens, no location-dependent variation was detected, such as between the Western and Eastern

Black Sea. Additionally, no effect of the Kızılırmak was found on the lower teeth. Species differ from each other in terms of each variation. Differences were detected when compared. It was also observed that there were species-specific characters (Table 2) and the dendrogram illustrating interspecies similarities and differences is provided in (Figure 5A).

### 4. Discussion

In this study, molar tooth variations were determined using genetically-diagnosed (mtDNA cytb and control region) *A. flavicollis* (n = 44), *A. witherbyi* (n = 19), *A. uralensis* (n = 27), *A. sylvaticus* (n = 7), and *A. mystacinus* (n = 37) samples, and the geographical distribution of these variations and the locations where the variations were observed were discussed. Dental characters obtained from the literature were examined for each specimen, and their presence/absence frequencies were used to categorize them into different regions. Furthermore, the aim was to differentiate *Apodemus* species with controversial taxonomic status based on these characteristics. In the study by Bellinvia (2004), the mitochondrial DNA control regions were examined to determine the relationship between different species within the genus *Apodemus*, and the species were placed into two subgenera: *Karstomys* (*A. epimelas* and *A. mystacinus*) and *Sylvaemus* (*A. alpicola*, *A. flavicollis*, *A. hermonensis*, *A. sylvaticus*, and *A. uralensis*). The proximity between *A. flavicollis* and *A. sylvaticus* and the separate branching of *A. mystacinus* observed in the study by Bellinvia (2004) are consistent with the morphological results in this study. In the study by Çolak (2007), which examined 253 samples from 45 different localities of the *Apodemus* genus in Türkiye using morphometric and biochemical analyses, it was found that *A. flavicollis* is genetically close to *A. sylvaticus* but distant from *A. mystacinus*. In this study, the morphological data obtained were found to be consistent (Figure 5A).

Tvrtković (1976) observed that the tubercle t9 in UM2 disappeared in *A. flavicollis* and revealed that the t12 variants showed a geographic distribution. In this study, all *A. flavicollis* samples had t9, and the occurrence of the t12 tubercle was relatively geographically distributed as in Tvrtković (1976), with a frequency of 66% in Anatolia and 53% in Thrace. Libois et al. (1993) found that the absence of t9 in the second upper molar was a diagnostic character for *A. flavicollis*, in contrast, in this study, we found t9 in UM2 of all genetically identified *A. flavicollis* samples. Kryštufek (2002) revealed that a specimen of *Mus sylvaticus witherbyi* Thomas, 1902 was synonymous with *A. witherbyi*. Kryštufek (2002) mentioned that the t1-t5 linkage is characteristic within the species *A. witherbyi*, but in the examined *A. flavicollis* samples in this study, the presence of t1-t5 linkage (D4) was found at a frequency



**Figure 5.** The UPGMA dendrograms based on nonmetric characters. A: Interspecific data, B: *A. flavicollis*, C: *A. mystacinus*.

**Table 2.** Interspecies comparison of the frequencies of variations within the species.

Species	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14
<i>A. flavicollis</i>	73%	61%	88%	52%	22%	44%	55%	41%	58%	0%	3%	25%	48%	48%
<i>A. sylvaticus</i>	57%	57%	57%	28%	57%	28%	71%	28%	71%	0%	14%	71%	33%	16%
<i>A. witherbyi</i>	0%	58%	76%	82%	58%	29%	70%	35%	64%	0%	35%	47%	5%	64%
<i>A. uralensis</i>	0%	5%	42%	26%	15%	31%	68%	0%	100%	0%	0%	7%	7%	35%
<i>A. mystacinus</i>	0%	88%	92%	0%	24%	84%	16%	72%	27%	100%	0%	13%	4%	33%

of 52%. Krystufek (2009) investigated samples of *A. flavicollis* from Anatolian Thrace and Gökçeada. While consistent results were obtained regarding the presence of t3 in UM1, an inconsistent outcome was observed concerning the presence of the t1 spur. Similarly, although the study suggested that t7 was generally straight, this study encountered a high incidence of pointed t7 cusps. Kryštufek et al. (2009), identified a morphological distinction between samples from Anatolia and Thrace. The observation of variations D1, D2, D4, and D13 in this study showing distinct ratios between samples from Anatolia and Thrace is consistent with the findings of Krystufek's (2009) (Figure 5B). On the other hand, lower teeth were examined, and we determined that no morphological difference was observed between Anatolia

and Thrace. Similar to morphological data, genetic differences have been detected (Selvi, 2019) between Anatolian and Thrace samples. Michaux et al. (2004), using the mtDNA cytb gene region, suggested that one of the main reasons for the genetic and morphological differentiation of *A. flavicollis* between Anatolian and Thrace populations is the presence of water barriers. The Dardanelles (Figure 1A), the Bosphorus (Figure 1B), and the Sea of Marmara form these barriers (Michaux et al., 2004; Michaux et al., 2005). Michaux et al. (2005) also showed that the isolation of Balkan and Anatolian populations due to early Pleistocene cooling contributed to the genetic differentiation of *A. mystacinus* and *A. epimelas*. Molecular clock analyses indicate that the divergence between these two groups occurred during the Tertiary-



Quaternary transition, approximately 2.2 to 2.4 million years ago, a period characterized by rapid and fluctuating climate differentiation throughout Europe. Along with changing climates, vegetation underwent transformations, leading to the emergence of a Northern European region dominated by steppe landscapes. *A. flavicollis* likely survived these early glaciation periods by adapting to forest habitats, possibly in the still-existing forests of the Mediterranean peninsula or the Middle East. It was also during this period that Balkan and Turkish *Erinaceus concolor* lineages diverged (Hewitt, 1999; Fauquette et al., 1998). Kankılıç et al. (2018) using mitochondrial DNA NADH dehydrogenase subunit 1 gene (ND1) analysis, determined the separation of *D. nitedula* lineages in Thrace and Anatolia.

Although *A. flavicollis* and *A. sylvaticus* often select the same or similar habitats, they are genetically distinguishable species despite the challenges in morphological differentiation (Michaux, 2004; Jojic et al., 2014). This study did not identify a dental surface pattern that could reliably separate *A. flavicollis* and *A. sylvaticus* samples. Mikulova and Frynta (2001) explained the similarity between *A. sylvaticus* and *A. flavicollis* based on measurements of body and skull characteristics. They attributed the similarity between *A. sylvaticus* and *A. flavicollis* to two different factors. According to Mikulova and Frynta (2001), firstly, both species showed high levels of variation within their own populations. Secondly, they suggested that closely related species with similar ecological needs and demands may not be able to coexist continuously due to competition, leading to the development of adaptive responses as a defense against the dominant competitor. In this context, the observed character changes were considered as an adaptive response displayed by the weaker species (Mikulova and Frynta, 2001). A study conducted in Italy (Amori and Contoli, 1994) highlighted that the morphometric diversity in *A. flavicollis* was greater than in *A. sylvaticus*, possibly due to competitive pressure. Furthermore, it emphasized the superiority of *A. flavicollis* over *A. sylvaticus* in this competition (Amori and Contoli, 1994). In this study, it was demonstrated for the first time that both *A. flavicollis* and *A. sylvaticus* share D1 characters (the presence of a bis in t2) within the genus, which is not found in other species.

When examining the UM1 structure, it was found that the t2 bis structure was present in all *A. flavicollis* in Thrace samples (n = 18), but this character is absent *A. flavicollis* samples from Anatolia. Similarly, in *A. sylvaticus* samples from Marmara Island and Gökçeada, the t2 bis structure (D1) was determined at 57%, while it was not observed in any of the Anatolian samples. The t4-t7 connection, which is almost characteristic of UM1 and UM2 in *A. sylvaticus* samples (Filippucci et al., 1996), was found at a rate of 57%

in UM1 and 71% in UM2 in this study. Kryštufek et al. (2009) mentioned that additional tubercles may be present between t1-t2 or t2-t3 and observed that t7 in UM1 could be straight or bulged and sometimes absent in *A. sylvaticus* samples collected from Greece and Edirne. However, no such tubercles were found in any of the samples of *A. sylvaticus* in this study and all specimens of *A. sylvaticus* had t7. Kryštufek (2002) examined a specimen of *A. sylvaticus creticus* Miller, 1910 and concluded that this species is synonymous with *A. sylvaticus* Linnaeus, 1758 based on morphological characters which is the t1-t5 structure was not observed in UM1 within *A. sylvaticus* species, while in this study, a t1-t5 connection was detected in 28% of UM1 samples.

*A. sylvaticus* populations from islands and Anatolia are clearly differentiated. When analyzing UM1 structure, it was observed that the t2 bis structure is unique to island populations. Additionally, while the t1-t5 connection is not observed in island samples, it is present in 66% of mainland (Anatolia) samples. In contrast, this study examined lower teeth, and it was determined that central distoconids in LM1 and LM2 are more developed in island populations but reduced in Anatolian populations. The reason for this situation could be due to the founder effect or genetic bottleneck resulting from genetic drift in the isolated island population (Chevret et al., 2021). In this study, *A. sylvaticus* samples from Gökçeada and Marmara Island overlap morphologically, but these two island populations are distinct from the mainland population. The differences between islands and mainland have been studied in many works using different techniques and species (Granjon and Cheylan (1990) for *Rattus rattus* based on skeletal measurements; Libois et al. (1993) for *A. sylvaticus* based on cranial characteristics; Michaux et al. (1996) *A. sylvaticus* based on mtDNA and allozyme studies; Renaud and Michaux (2007) *A. sylvaticus* based on mandible and first upper molar surface outline analysis. The samples whose morphological characteristics were investigated in this study were also genetically analyzed by Selvi (2019), revealing that all samples from Western Anatolia clustered together with Gökçeada, Thrace, and European populations. Additionally, in the study conducted by Özkan (1999), the similarity of *Apodemus* samples with Gökçeada and Anatolia was revealed. This supports the hypothesis that *A. sylvaticus* samples in Gökçeada originated from Thrace. The overlapping of fundamental morphological characters in Gökçeada and Marmara Island samples also suggests the expansion of *A. sylvaticus* from Thrace to Marmara Island. The swollen structure of t7 in the first upper molar is common in Anatolia and Marmara Island. Yaltırak et al. (2002) proposed that Marmara Island was connected to Thrace and Anatolia through a land bridge during the Pleistocene period. However, after the

Messinian Salinity Crisis (5.96–5.33 Mya), the opening of the Strait of Gibraltar was determined to have interrupted the connection between the Mediterranean and the Black Sea during the Pliocene (5.33–3.5 Mya) period, which may have severed the connection between Marmara Island and Thrace-Anatolia (Popov et al., 2004; Çağatay et al., 2006). Global sea level rise and increased activity on the North Anatolian Fault (Çağatay et al., 2006) could have cut off the connection between Marmara Island, Thrace, and Anatolia. These results are based on a little sample set ( $n = 7$ ) of *A. sylvaticus*. This indicates the need for further testing of *A. sylvaticus* populations with more samples. These results indicate the need for further testing of *A. sylvaticus* populations with more samples.

Among *A. witherbyi* samples distributed in Anatolia, Thrace, and Bozcaada, it was determined that Bozcaada differs from both Anatolian and Thrace samples, despite the similarity between Bozcaada and Thrace samples with several distinct variations. The t4-t7 connection in UM1 is quite common in Thrace and Bozcaada, while it is only present in 25% of Anatolian samples. Similarly, the straightness of t7 in UM2 (D9) is more prevalent in Thrace and Bozcaada, while it is relatively less common in Anatolia. Özkan and Kryštufek (1999) indicated the similarities between Bozcaada and Northwestern Anatolian samples. Selvi (2019) revealed in genetic analysis studies of these samples with examined morphological characters that Bozcaada samples belong to a different lineage and demonstrated recent gene flow between Thrace and Bozcaada. Bozcaada samples exhibit distinct characteristics from both mainland and Thrace. The presence of t12 in UM1 is less common in Bozcaada compared to Anatolian and Thrace samples, and similarly, the pointedness of t7 in UM1 is observed in 60% of Bozcaada samples, while it is less frequent in mainland samples. In UM3, the t6-t8 connection is observed in all island samples but only in half of the mainland samples. This may point possible bottleneck effect (Chevret et al., 2021) for *A. witherbyi* in Bozcaada.

In Kryštufek (2009) study, *A. witherbyi* samples from Antalya, Sivas, Zonguldak, and Konya were examined, and it was proposed that the t7 tubercle in UM1 is pointed, wide, and developed and t12 is occasionally observed in UM2. However, this finding was found to be inconsistent with the results of this study, which utilized genetically diagnosed *A. witherbyi* samples from Anatolia. Nevertheless, the high frequency of the t1-t5 connection in UM1 observed in Kryštufek's (2009) study remains consistent.

In *A. uralensis* samples, when the area between Bursa and Ordu (excluding Ordu) was considered as Western Black Sea and the region between Ordu and Ardahan (including Ordu) was considered as Eastern Black Sea, no sharp distinction was observed in the morphology

of the lower and upper molar teeth. Only in the Eastern Black Sea region, it was found that the straightness of t7 is a rarer occurrence compared to the Western Black Sea. These slight differences between the East and West regions may be due to variations in vegetation and temperature. Filippucci et al. (1996) stated that t12 is absent in *A. uralensis*. In contrast to Filippucci et al. (1996), t12 was found in 14% of the samples in this study. Kryštufek et al. (2009) stated, for samples collected from Bolu, Zonguldak, and Artvin, that the t1-t5 connection was not observed in UM1 within the species. In this study, a t1-t5 connection was found in 26% of the examined samples. Kryštufek et al. (2009) also mentioned that the wide form of t7 is rare and t12 in UM2 is a less common character. Similarly, in this study, it was observed that the wide form of t7 is rare, being with consistent with Kryštufek et al. (2009). However, in contrast to Kryštufek et al. (2009), t12 was not observed in any of the samples of *A. uralensis* in this study.

In the study by Kryštufek and Vohlarik (2007), they collected *A. uralensis* samples from 19 different localities in Northern Anatolia and morphologically diagnosed the species. They found that the t1-t5 connection is absent in UM1, t1bis is not present in UM1, and t7 is straight in UM1. In this study, no t1bis was found in any of the samples in UM1, and t7 in UM2 was determined to be straight in 100% of the cases. This finding is consistent with the study by Kryštufek and Vohlarik (2007). However, in this study, a t1-t5 connection was found in 26% of *A. uralensis* samples in UM1, which is not in line with the study by Kryštufek and Vohlarik (2007). This discrepancy could be due to differences in localities.

The differentiating effect of the Kızılırmak, which is within the distribution range of *A. uralensis* (Figure 1C), was investigated, and based on morphological data in this study, it was determined that the eastern and western populations are not different. Helvacı et al. (2012) investigated the distribution and differentiation of *Glis glis* samples using mtDNA cytb and UM1 shape variations (geometric morphometrics). Helvacı et al. (2012) found no genetic differences between Anatolian and Thrace population based on mtDNA cytb sequences. On the basis of geometric morphometrics of UM1, they revealed that Anatolia differs from Thrace and the Melet River separates the population. In this study, *A. uralensis* samples were examined as the Western Black Sea group between Bursa and Ordu and the Eastern Black Sea group between Ordu and Ardahan. Contrary to Helvacı et al. (2012) this study was found that the Melet River, located between the two groups (Figure 1D), separates the *A. uralensis* samples with very small differences into Eastern and Western forms.

Kankılıç et al. (2018) analyzed *D. nitedula* samples using ND1 gene sequences. The researchers revealed that two different lineages of *D. nitedula* are present east

and west of the Çoruh River. However, in this study, *A. uralensis* samples from the eastern and western regions of the Çoruh River (Figure 1.E) were compared in terms of dental characteristics, and no differences were detected. Selvi (2019) determined in their study that the same *A. uralensis* samples did not undergo a genetic interruption by the rivers and streams of Northern Anatolia and that there was no distinction between East and West.

In all examined samples of *A. mystacinus*, the presence of t12 in UM1 and UM2 can be considered as a characteristic feature of the species (Kryštufek et al., 2009). In this study, *A. mystacinus* samples were divided into two distinct groups, namely the Western Black Sea Region and Eastern Black Sea Region, based on dental morphology. The t3 spur was observed in all Eastern Black Sea samples, while it was less common in Western Black Sea samples. Similarly, the t4-t7 connection was observed in Eastern Black Sea samples but absent in Western Black Sea samples. The t4-t7 connection in UM2 is widespread among Western Black Sea samples. Selvi (2019) also revealed a similar differentiation between the Western and Eastern Black Sea regions based on the genetic status of the same samples.

Kastamonu, Düzce, and Zonguldak provinces were considered part of the Western Black Sea region, located west of the Kızılırmak (Figure 1C). The fact that all the investigated Eastern provinces are located in the east of the Kızılırmak suggests that the river acts as a barrier separating *A. mystacinus* populations (Figure 5C). Quaternary tectonic activities and changes in sea level during glacial or interglacial periods contributed to delta formation during the Holocene (Turoğlu, 2010), causing interruptions in Northern Anatolian forest habitats and leading to habitat fragmentation, which may have disrupted gene flow between populations (Çolak et al., 2016). Similarly, Çolak et al. (2016), Olgun Karacan and

Beteş (2019), and Olgun Karacan et al. (2021) divided *A. mystacinus* populations in Northern Anatolia into two distinct groups, Eastern and Western lineages, using mtDNA cytb and mtDNA control region, as well as SSRs gene regions. To further confirm this, it is important to conduct a broader study in the region.

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#### Author contributions

All the authors have accepted responsibility for the entire content of this submitted manuscript and approved submission.

#### Conflict of interest statement

The authors declare no conflicts of interest regarding this article.

#### Research ethics

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#### Data availability

Authors declare that; materials (skulls and skull's photographs) used in this study are available in Ankara University Mammalian Research Collection in Faculty of Science, Biology Department (AUMAC). <https://mammalia.ankara.edu.tr/>

## References

- Adler GH, Levins R (1994). The island syndrome in rodent populations. *The Quarterly review of biology* 69 (4): 473-490. <https://doi.org/10.1086/418744>
- Amori G, Contoli L (1994). Morphotypic, craniometric and genotypic diversification in *Apodemus flavicollis* and *Apodemus sylvaticus*. *Bolletino di zoologia* 61 (4): 353-357. <https://doi.org/10.1080/11250009409355906>
- Bellinva E (2004). A phylogenetic study of genus *Apodemus* by sequencing the mitochondrial DNA control region. *Journal of Zoological Systematics and Evolutionary Research* 42: 289-297. <https://doi.org/10.1111/j.1439-0469.2004.00270.x>
- Chevret P, Hautier L, Ganem G, Herman J, Agret S et al. (2021). Genetic structure in Orkney Island mice: isolation promotes morphological diversification. *Heredity* 126 (2): 266-278. <https://doi.org/10.1038/s41437-020-00368-8>
- Çağatay NM, Görür N, Flecker R, Sakıncı M, Tünoğlu C et al. (2006). Paratethyan-Mediterranean 183 connectivity in the Sea of Marmara region (NW Turkey) during the Messinian. *Sedimentary Geology* 188 (3): 171-187. <https://doi.org/10.1016/j.sedgeo.2006.03.004>
- Çolak R, Çolak E, Yiğit N (2005). Morphometric, Karyotypic and Electrophoretic Analysis of the Genus *Apodemus* Kaup, 1826 (Mammalia: Rodentia) in Thrace. *Turkish Journal of Zoology* 29 (2): 147-153.
- Çolak R, Çolak E, Yiğit N, Kandemir İ, Sözen M (2007). Morphometric and Biochemical Variation and the Distribution of the Genus *Apodemus* (Mammalia: Rodentia) in Turkey. *Acta Zoologica Academiae Scientiarum Hungaricae* 53 (3): 239-256.

- Çolak R, Kandemir I, Olgun Karacan G, Kankılıç T, Çolak E et al. (2013). Allozyme variation in bank vole, *Myodes glareolus* (Mammalia: Rodentia) in Northern Anatolia. *Biochemical Systematics and Ecology* 50: 304-309. <https://dx.doi.org/10.1016/j.bse.2013.04.013>
- Çolak R, Olgun Karacan G, Kandemir I, Çolak E, Kankılıç T et al. (2016). Genetic variations of Turkish bank vole, *Myodes glareolus* (Mammalia: Rodentia) inferred from mtDNA. *Mitochondrial DNA. Part A, DNA mapping, sequencing, and analysis*, 27 (6): 4372-4379. <https://doi.org/10.3109/19401736.2015.1089537>
- Ellerman JR (1941). *The families and genera of living rodents*. Oxford Univ. Press., 1-644, London.
- Fauquette S, Guiot J, Suc JP (1998). A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Paleogeography, Palaeoclimatology, Palaeoecology* 144 (1): 183-201. [https://doi.org/10.1016/S0031-0182\(98\)00083-2](https://doi.org/10.1016/S0031-0182(98)00083-2)
- Filippucci MG, Storch G, Macholán M (1996). Taxonomy of the genus *Sylvaemus* in western Anatolia - morphological and electrophoretic evidence (Mammalia: Rodentia: Muridae). *Senckenbergiana biologica* 75: 1-14.
- Filippucci MG, Macholán M, Michaux JR (2002). Genetic variation and evolution in the genus *Apodemus* (Muridae: Rodentia). *Biological Journal of the Linnean Society* 75(3):395-419.
- Frynta D, Mikulová P, Suchomelová E, Sádlova J (2001). Discriminant analysis of morphometric characters in four species of *Apodemus* (Muridae: Rodentia) from eastern Turkey and Iran. *Israel Journal of Zoology* 47 (3): 243-258.
- Frynta D, Mikulová P, Vohralík V (2006). Skull shape in the genus *Apodemus*: phylogenetic conservatism and/or adaptation to local conditions. *Acta Theriologica* 51: 139-153. <https://doi.org/10.1007/BF03192665>
- García-Rodríguez O, Andreou D, Herman JS et al. (2018). Cyprus as an ancient hub for house mice and humans. *Journal of Biogeography* 45 (12): 2619-2630 <https://doi.org/10.1111/jbi.13458>
- Granjon L & Cheylan G (1990). Differentiation biometrique des rats noirs (*Rattus rattus*) des lies ouest-mediterraneennes. *Mammalia* 54 (2): 213-232. <https://doi.org/10.1515/mamm-1990-0206>
- Helvacı Z, Renaud S, Ledevin R, Adriaens D, Michaux J et al. (2012). Morphometric and genetic structure of the edible dormouse (*Glis glis*): a consequence of forest fragmentation in Turkey. *Biological Journal of the Linnean Society* 107 (3): 611-623. <https://doi.org/10.1111/j.1095-8312.2012.01952.x>
- Hewitt GM (1999). Post-glacial recolonization of European Biota. *Biological Journal of the Linnean Society* 68 (1-2): 87-112. <https://doi.org/10.1111/j.1095-8312.1999.tb01160.x>
- Javidkar M, Darvish J, Bakhtiari AR (2007). Morphological and morphometric analyses of dental and cranial characters in *Apodemus hyrcanicus* and *A. wetherbyi* (Rodentia: Muridae) from Iran. *Mammalia* 71 (1-2): 56-62. <https://doi.org/10.1515/MAMM.2007.010>
- Jojic V, Bugarski-Stanojevic V, Blagojevic J, Vujosevic M (2014). Discrimination of the sibling species *Apodemus flavicollis* and *A. sylvaticus* (Rodentia, Muridae). *Zoologischer Anzeiger* 253 (4): 261-269. <https://doi.org/10.1016/j.jcz.2014.02.002>
- Kankılıç T, Şeker PS, Erdik AC, Kankılıç T, Selvi E et al. (2018). Determination of genetic variations in the genus *Dryomys* Thomas, 1906 (Rodentia: Gliridae) distributed in Turkey using NADH dehydrogenase 1 (ND1) gene. *Mitochondrial DNA Part A* 29 (6): 933-942. <https://doi.org/10.1080/24701394.2017.1389915>
- Kryštufek B (2002). Identity of four *Apodemus* (*Sylvaemus*) types from the eastern Mediterranean and the Middle East. *Mammalia* 66 (1): 43-52. <https://doi.org/10.1515/mamm.2002.66.1.43>
- Kryštufek B, Vohralík V (2007). Distribution of field mice (*Apodemus*) (Mammalia: Rodentia) in Anatolia. *Zoology in the Middle East* 42 (1): 25-36. <https://doi.org/10.1080/09397140.2007.10638243>
- Kryštufek B, Vohralík V (2009). *Mammals of Turkey and Cyprus: Rodentia II: Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae, Castoridae*. University of Primorsca, Science and research center Koper, Koper.
- Lack D (1976). *Island Biology: Illustrated by the Land Birds of Jamaica*. Blackwell Scientific Publications, Oxford. <https://doi.org/10.2307/2418771>
- Libois R, Fons RA, Bordenave D (1993). Mediterranean small mammals and insular syndrome: biometrical study of the long tailed field mouse (*Apodemus sylvaticus*) (Rodentia Muridae) of Corsica. *Bonner Zoologische Beiträge* 44 (3-4): 147-163
- Michaux JR, Filippucci MG, Libois RM, Fons R, Matagne RF (1996). Biogeography and taxonomy of *Apodemus sylvaticus* (the woodmouse) in the Tyrrhenian region: enzymatic variations and mitochondrial DNA restriction pattern analysis. *Heredity* 76 (3): 267-277. <https://doi.org/10.1038/hdy.1996.40>
- Michaux JR, Libois R, Filippucci MG (2004). So close and so different: comparative phylogeography of two small mammal species, the Yellow necked fieldmouse (*Apodemus flavicollis*) and the Woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. *Heredity* 94 (1): 52-63. <https://doi.org/10.1038/sj.hdy.6800561>
- Michaux J, Bellinva E, Lymberakis P (2005). Taxonomy, evolutionary history, and biogeography of the broad-toothed field mouse (*Apodemus mystacinus*) in the eastern Mediterranean area based on mitochondrial and nuclear genes. *Biological Journal of the Linnean Society* 85 (1): 53-63. <https://doi.org/10.1111/j.1095-8312.2005.00469.x>
- Mikulová P, Frynta D (2001). Test of character displacement in urban populations of *Apodemus sylvaticus*. *Canadian Journal of Zoology* 79 (5): 794-801. <https://doi.org/10.1139/z01-035>
- Olgun Karacan G, Beteş D (2019). Determination of Genetic Diversity in *Apodemus mystacinus* (Mammalia: Rodentia) based on SSRs. *Iğdır Üniversitesi Fen Bilimleri Enstitüsü Dergisi* 9 (2): 1098-1108. <https://doi.org/10.21597/jst.409142>

- Olgun Karacan G, Çolak R, Çolak E (2021). The roles of possible geographic barriers and geological events on the phylogeographic structure of the Eastern broad toothed field mouse (*Apodemus mystacinus*). *Mammalia* 85 (5): 401-411. <https://doi.org/10.1515/mammalia-2020-0017>
- Özkan B, Kryštufek B (1999). Wood mice, *Apodemus* of two Turkish islands: Gökçeada and Bozcaada. *Folia Zoologica* 48 (1): 17-24.
- Özkan B (1999). Rodent Fauna of Imbros and Tenedos (Mammalia: Rodentia). *Turkish Journal of Zoology* 23 (5): 133-147
- Popov SV, Rögl F, Rozanov AY, Steininger FF, Shcherba IG et al. (2004). Lithological-Palaeogeographic maps of Paratethys. *CFS Courier Forschungsinstitut Senckenberg* 250: 1-46.
- Renaud S (2005). First upper molar and mandible shape of wood mice (*Apodemus sylvaticus*) from northern Germany: ageing, habitat, and insularity. *Mamm. biol.* 70 (3): 157-170. <https://doi.org/10.1016/j.mambio.2004.10.004>
- Renaud S, Michaux JR (2007). Mandibles and molars of the wood mouse, *Apodemus sylvaticus* (L.): integrated latitudinal pattern and mosaic insular evolution. *Journal of Biogeography* 34 (2): 339-355. <https://doi.org/10.1111/j.1365-2699.2006.01597.x>
- Selvi E (2019). Kuzey Anadolu ve Trakya'daki *Apodemus* Kaup, 1829 (Mammalia: Rodentia) Cinsine Ait Türlerin Mitokondriyal DNA (Sitokrom b ve Kontrol Bölgesi) Analizi. Doktora Tez, Ankara Üniversitesi, Fen Bilimleri Enstitüsü, Biyoloji Anabilim Dalı, Ankara (in Turkish).
- Siahsarvie R, Darvish J (2008). Geometric morphometric analysis of Iranian wood mice of the genus *Apodemus* (Rodentia, Muridae). *Mammalia* 72 (2): 109-115. <https://doi.org/10.1515/MAMM.2008.020>
- Turoğlu H (2010). Geomorphological characteristics of Kızılırmak delta and immediate environment and their impact on human live. İstanbul University, Faculty of Letters, Anatolian Research 19: 99-111.
- Tvrkovic N (1976). The variability of the postero external supplemental tubercle t12 on the 1st and 2nd upper molars in the species *Apodemus sylvaticus* and *Apodemus flavicollis* from western yugoslavia. *Periodicum Biologorum* 78: 91-100.
- Ungar PS (2015). Mammalian dental function and wear: a review. *Biosurface and Biotribology* 1 (1): 25-41. <https://doi.org/10.1016/j.bsbt.2014.12.001>
- Williamson M (1981). *Island Populations*. Oxford University Press, Oxford.
- Wilson DE, Reeder DM (2005). *Mammal Species of the World. A Taxonomic and Geographic Reference*. Johns Hopkins University Press. <https://doi.org/10.56021/9780801882210>
- Yaltırak C, Sakiç M, Aksu AE, Hiscott RN, Galle B et al. (2002). Late Pleistocene uplift history along the southwestern Marmara Sea determined from raised coastal deposits and global sea-level variations. *Marine Geology* 190 (1-2): 283-305 [https://doi.org/10.1016/S0025-3227\(02\)00351-1](https://doi.org/10.1016/S0025-3227(02)00351-1)
- Zykov S, Izvarin E (2020). Variations in dental morphologies of yellow-necked mouse (*Apodemus flavicollis* Melchior, 1834) from Nizhneirginsky Grotto sediments (Middle Urals) in a phylogeographical context. *Quaternary International* 546: 152-159. <https://doi.org/10.1016/j.quaint.2019.11.007>

**Supplementary Appendix.** Work samples and locations.

Location	n	Species	Map number
Trabzon-Yomra	1	<i>Apodemus flavicollis</i>	4
Giresun-Barça-Merkez	1	<i>Apodemus flavicollis</i>	5
Giresun-Bulancak	1	<i>Apodemus flavicollis</i>	5
Ordu-Akkuş	1	<i>Apodemus flavicollis</i>	6
Ordu-Perşembe-Efirli	2	<i>Apodemus flavicollis</i>	6
Samsun-Çakallı	1	<i>Apodemus flavicollis</i>	8
Çorum-20km kuzey	3	<i>Apodemus flavicollis</i>	10
Zonguldak	3	<i>Apodemus flavicollis</i>	12
Sinop-Bürnük	1	<i>Apodemus flavicollis</i>	9
Çanakkale-Biga-Sinekçi	1	<i>Apodemus flavicollis</i>	22
Bursa-Uludağ	1	<i>Apodemus flavicollis</i>	17
Bolu-Abant	1	<i>Apodemus flavicollis</i>	13
Kocaeli-Kartepe	3	<i>Apodemus flavicollis</i>	15
İstanbul-Beykoz	6	<i>Apodemus flavicollis</i>	16
Edirne-Azatlı	4	<i>Apodemus flavicollis</i>	21
Edirne-Enez	3	<i>Apodemus flavicollis</i>	21
Çanakkale-Gelibolu-Sütlüce	1	<i>Apodemus flavicollis</i>	22
Tekirdağ-Kumbağ-Naip Köyü	5	<i>Apodemus flavicollis</i>	18
Tekirdağ-Çerkezköy	3	<i>Apodemus flavicollis</i>	18
Kırklareli-Lüleburgaz	2	<i>Apodemus flavicollis</i>	19
Total	44		

Location	n	Species	Map number
Edirne-Orhaniye-Bağlık	3	<i>Apodemus witherbyi</i>	21
Tekirdağ-Kumbağ-Naip Köyü	1	<i>Apodemus witherbyi</i>	18
Çanakkale-Gelibolu-Fındıklı	2	<i>Apodemus witherbyi</i>	22
Çanakkale-Gelibolu-Sütlüce	4	<i>Apodemus witherbyi</i>	22
Çanakkale-Bozcaada	5	<i>Apodemus witherbyi</i>	22
Çorum-20km kuzey	1	<i>Apodemus witherbyi</i>	10
Samsun-Kurupelit	2	<i>Apodemus witherbyi</i>	8
Çanakkale-Biga-Sinekçi	1	<i>Apodemus witherbyi</i>	22
Total	19		

Location	n	Species	Map number
Çanakkale-Gökçeada-Uğurlu	2	<i>Apodemus sylvaticus</i>	22
Balıkesir-Marmara Adası	2	<i>Apodemus sylvaticus</i>	20
Samsun-Kurupelit	3	<i>Apodemus sylvaticus</i>	8
Total	7		

Location	n	Species	Map number
Bursa-Uludağ	1	<i>Apodemus uralensis</i>	17
Kocaeli-Kartepe	2	<i>Apodemus uralensis</i>	15
Düzce-Akçakoca	1	<i>Apodemus uralensis</i>	14
Sinop-Bürnük	3	<i>Apodemus uralensis</i>	9
Sinop-Dikmen-Göktepe	2	<i>Apodemus uralensis</i>	9
Ordu-Akkuş	1	<i>Apodemus uralensis</i>	6
Trabzon-Maçka-Sümela	5	<i>Apodemus uralensis</i>	4
Rize-Çayeli-Çataldere	5	<i>Apodemus uralensis</i>	3
Rize-Çamlıhemşin	1	<i>Apodemus uralensis</i>	3
Artvin-Karagöl Milli Parkı	3	<i>Apodemus uralensis</i>	2
Artvin-Hopa	1	<i>Apodemus uralensis</i>	2
Ardahan-Posof	2	<i>Apodemus uralensis</i>	1
Total	27		

Location	n	Species	Map number
Kastamonu-Hanönü	1	<i>Apodemus mystacinus</i>	11
Düzce-Akçakoca-Akkaya	2	<i>Apodemus mystacinus</i>	14
Zonguldak	3	<i>Apodemus mystacinus</i>	7
Tokat-Pazar-Kalederesi	3	<i>Apodemus mystacinus</i>	12
Giresun-Bulancak	6	<i>Apodemus mystacinus</i>	5
Trabzon-Maçka-Sümela	5	<i>Apodemus mystacinus</i>	4
Trabzon-Sürmene	1	<i>Apodemus mystacinus</i>	4
Rize-Çamlıhemşin	6	<i>Apodemus mystacinus</i>	3
Artvin-Cankurtaran Geçidi	3	<i>Apodemus mystacinus</i>	2
Artvin-Hopa	1	<i>Apodemus mystacinus</i>	2
Artvin-Ardanuç	6	<i>Apodemus mystacinus</i>	2
Total	37		