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New Data on the Taxonomy of the Genus *Apodemus* Kaup, 1829 (Mammalia: Rodentia) in Turkey: a Geometric Morphometric Approach

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Abstract: Morphometric relationships among 338 specimens of species of the genus *Apodemus* representing 17 localities and their neighbourhoods from North Anatolia and Turkish Thrace were explored. Taxonomic relations of *Apodemus* were analysed by using outline geometric morphometrics based on the first upper molar for the first time, thus aiming to have a better understanding of size and shape variations separately. *Apodemus agrarius* (subgenus *Apodemus*) was identified as a more differentiated species in terms of shape analysis. *Apodemus mystacinus* (subgenus *Karstomys*) differentiation was especially obvious for molar size but clustered close together with species of *Sylvaemus* in the morphospace. The outcome of this study confirms the presence of taxonomic complexity among species of the subgenus *Sylvaemus*.

Key words: *Apodemus,* outline analysis, Thrace, Northern Anatolia

Introduction

In the genus *Apodemus* Kaup, 1829, previous studies, using diverse methods and with no certain preciseness, identified from 14 to 21 species (Musser & Carleton 1993, Musser & Carleton 2005, Wilson & Reeder 2005), almost 35 subspecies and from two to four subgenera. New species are still being discovered (Ge et al. 2019). There is not a consensus on the taxonomy of the genus *Apodemus* despite the recently improved methods. There are various opinions on the taxonomic arrangement of the groups that belong to this genus. According to Zimmermann (1962), there are three subgenera based on morphological characters (the existence or non-existence of supraorbital ridges, molar morphology, etc.). In their studies, Musser et al. (1996) revised the question of the taxonomic relationships between *Apodemus* and *Sylvaemus* by analysing 4296 Oriental and 90 European samples from numerous museums in America and Europe, together with unrecorded European samples and using the published morphological and genetic data. Musser et al. (1996) classified the genus into three subgenera: *Apodemus*, *Sylvaemus* (including *A. mystacinus*) and *Argenteus*. To support such distinction, there were studies on protein electrophoresis (Filippucci et al. 2002). Serizawa et al. (2000) divided the genus *Apodemus* into four groups by using phylogenetic markers (cytochrome *b* and IRBP): (1) *Agrarius* group (*Apodemus agrarius*, *Apodemus peninsulae*, *Apodemus semotus* and *Apodemus speciosus*), (2) *Argenteus* group (*Apodemus argenteus*), (3) *Gurkha* group (*Apodemus gurkha*) and (4) *Sylvaticus* group (*Apodemus alpicola*, *Ap-*

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odemus flavicollis and *Apodemus sylvaticus*). This is quite compatible with the morphological studies by Serizawa et al. (2000) and Musser et al. (1996). Unlike Musser et al. (1996), Serizawa et al. (2000) did not include *A. gurkha* in the group of the other Asian species but placed it in an independent group.

Besides all these approaches, there are many phylogenetic and systematic studies on *Apodemus* (e.g., Filippucci et al. 1996, Michaux et al. 2002, Çolak et al. 2007, Kryštufek et al. 2009, Jojić et al. 2014, Martin Cerezo et al. 2020). Six species occur across Turkey: *Apodemus sylvaticus* (Linnaeus, 1758), *A. agrarius* (Pallas, 1771), *A. uralensis* (Pallas, 1811), *A. flavicollis* (Melchior, 1834), *A. mystacinus* (Danford & Alston, 1877) and *A. witherbyi* (Thomas, 1902).

As indicated in the above summary, it is clear that the morphological and genetic analyses are insufficient in solving the taxonomic problems within the genus *Apodemus*. This is especially valid for the species of the subgenus *Sylvaemus*. Morphometrical studies on *Apodemus* in Turkey (e. g. Frynta et al. 2001, Çolak et al. 2007) have been limited to traditional morphometrics, which has been a useful tool for many years (Zelditch et al. 2004). However, by using geometric morphometrics, while shape and size can be analysed in different analyses, the changes in different parts of the analysed groups can also be extensively compared and contrasted (MacLeod & Forey 2002). Therefore, in this study, outline analyses were carried out for the first time in order to reveal the relationships among six species of *Apodemus* occurring in the north of Turkey. We also explore how outline geometric morphometrics contribute to the taxonomy of this group based on the first upper molar.

Materials and Methods

We collected 338 specimens of the genus *Apodemus* in 1991–2009 from 17 localities in the northern Anatolia and Thrace (Fig. 1). For detailed data on samples, see Table 1. All individuals were considered adults or sub-adults based on the criterion that the third molars were fully erupted as a result of weaning. Males and females were pooled as no sexual dimorphism had been documented for tooth morphology in adults and sub-adults (Helvaci 2012). Besides the samples taken from the area of this study, samples from the Aegean, Mediterranean, Middle Anatolian and South-East Anatolian (n=30) regions of Turkey were photographed, analysed and used as a material for identification. In addition, Muséum National d'Histoire Naturelle (MNHN) (Paris, France) was visited and the samples of *Apodemus* were photographed via portable display system.

The taxonomy of the six species of *Apodemus*, which were identified according to their morphological characteristics, was re-assessed. Comparison of museum samples with genetic descriptions and contributions of literature (Filippucci et al. 1996,

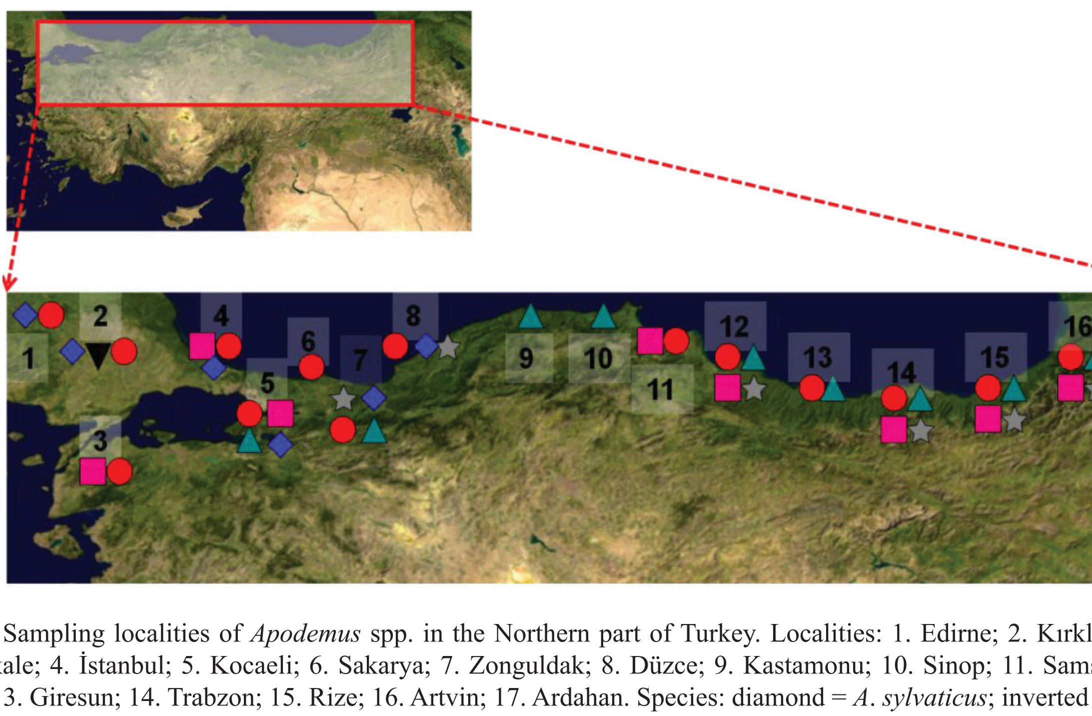

Fig. 1. Sampling localities of *Apodemus* spp. in the Northern part of Turkey. Localities: 1. Edirne; 2. Kırklareli; 3. Çanakkale; 4. İstanbul; 5. Kocaeli; 6. Sakarya; 7. Zonguldak; 8. Düzce; 9. Kastamonu; 10. Sinop; 11. Samsun; 12. Ordu; 13. Giresun; 14. Trabzon; 15. Rize; 16. Artvin; 17. Ardahan. Species: diamond = *A. sylvaticus*; inverted triangle = *A. agrarius*; triangle = *A. uralensis*; circle = *A. flavicollis*; star = *A. mystacinus*; square = *A. witherbyi*.

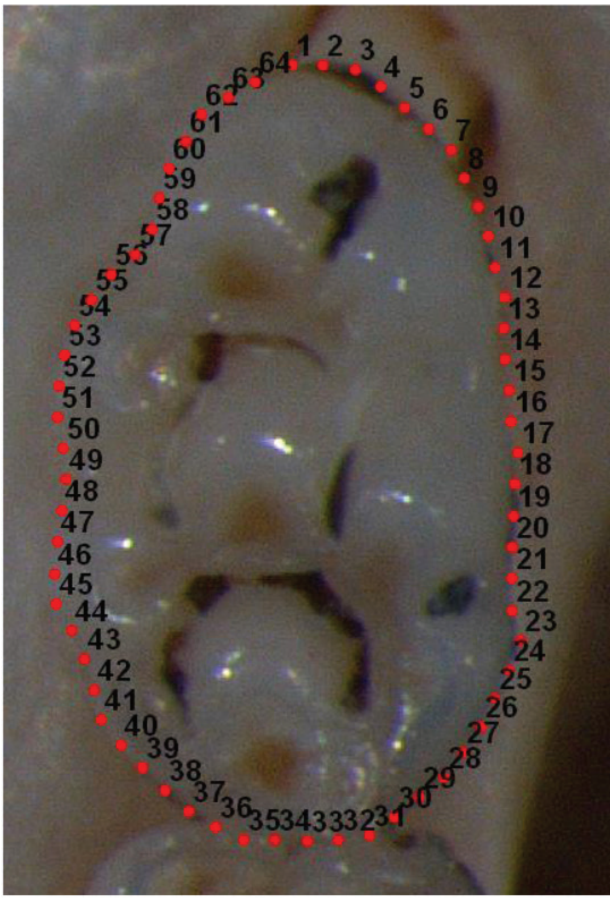

Fig. 2. First upper molar of *Apodemus* in occlusal view. The studied outline is superimposed on the first upper molar (UM1), with the starting point (1) at the maximum curve of the UM1 (Lingual side to the left, anterior part to the top).

Krystufek & Vohralík 2007, Darvish et al. 2014) was carried out.

For morphological examination, the skulls were first placed on small glass spheres and then on a Leica MZ 16 stereomicroscope with a Leica DFC 320 camera. Via proper lighting, they were visually examined and images were transferred to the computer. For each surface, the most suitable magnification was captured through analysis. For the outline of each tooth, the coordinates of 64 *x* and *y*, evenly distributed round the teeth, were recorded via TpsDig. The starting point of the contour was generally determined to be the maximum skewness of the frontal part of the tooth (Fig. 2). Sixty-four radii observed in these coordinates were calculated; the distance of the 64 points defining the tooth contour corresponded to the centre of gravity. Then, the Fourier Transform was applied to this 64-point radius set. Thus, the outline was expressed as the sum of such trigonometric functions as the increasing wavelengths. The first seven harmonics and their

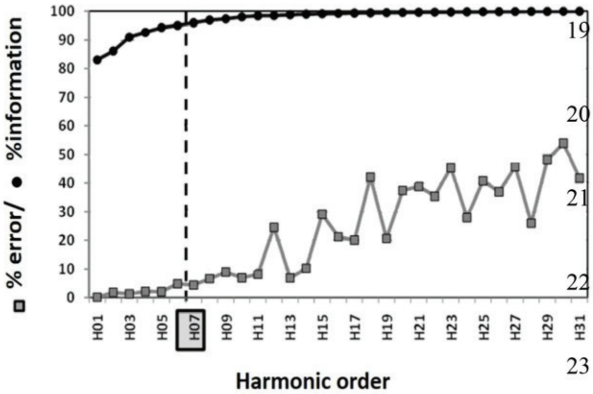

Fig. 3. Measurement error (grey square) and cumulative power (black dots) as a function of the harmonic order for the elliptic Fourier transform of the *Apodemus* first upper molar outline. The measurement error is expressed as the coefficient of variation of the harmonic amplitude (= square root of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

morphological details that were biologically significant were preserved without loss of information. It was determined that the selection of the harmonic for the analysis of the following samples in the EFAWin program would be seven (Fig. 3).

In order to determine the sufficient harmonic number for *Apodemus*, the first upper molar (UM1) shape that belonged to a tooth was measured ten times and an estimated margin of error was calculated for each harmonic (Fig. 3). Measurement error was obtained by evaluating the percentage of error for the amplitude of each harmonic (Fourier coefficients, FCs), square root of the sum of the squares *An, Bn, Cn* and *Dn*). Measurement error for the first molar tooth of *Apodemus* was detected to be lower than 5% in the seventh harmonic (Fig. 3). Each of the first seven harmonics included 96% of the whole information on shape. Following harmonics (8 and up) were not preferred since they did not provide purposive information on shape. As a function of the first upper molar Elliptic Fourier Transform harmonic order of the genus *Apodemus*, measurement error (grey squares) and cumulative force (black circles) are displayed (Fig. 3).

Cluster analysis was performed using the first axis of canonical analysis (CA1) values of the differentiation analysis results obtained for the first upper molar and it was calculated based on Euclidean distances. Systat Ver 13.0 was used for all statistical analyses.

Table 1. Sample distribution based on species, latitude, longitude for each locality (N_{UM1}= sample size of first upper molar)

Species	Locality	Latitude	Longitude	N_{UM1}
A. sylvaticus	Edirne	41°40'N	26°34'E	5
A. sylvaticus	Kırklareli	41°49'N	27°45'E	14
A. sylvaticus	Istanbul	41°07'N	29°06'E	2
A. sylvaticus	Kocaeli	40°54'N	30°03'E	4
A. sylvaticus	Düzce	41°05'N	31°07'E	1
A. sylvaticus	Zonguldak	41°13'N	31°57'E	1
A. agrarius	Kırklareli	41°53'N	27°59'E	12
A. uralensis	Kocaeli	40°42'N	30°05'E	2
A. uralensis	Düzce	41°05'N	31°07'E	1
A. uralensis	Kastamonu	41°09'N	34°03'E	7
A. uralensis	Sinop	42°01'N	35°09'E	4
A. uralensis	Ordu	40°47'N	37°00'E	4
A. uralensis	Trabzon	40°50'N	39°46'E	12
A. uralensis	Rize	41°04'N	40°48'E	12
A. uralensis	Artvin	41°21'N	41°40'E	6
A. uralensis	Ardahan	41°30'N	42°43'E	1
A. flavicollis	Edirne	41°40'N	26°34'E	2
A. flavicollis	Kırklareli	41°53'N	27°59'E	9
A. flavicollis	Çanakkale	40°09'N	26°24'E	1
A. flavicollis	Istanbul	41°10'N	29°36'E	16
A. flavicollis	Kocaeli	40°54'N	30°03'E	7
A. flavicollis	Sakarya	41°06'N	30°41'E	2
A. flavicollis	Zonguldak	41°13'N	31°57'E	7
A. flavicollis	Düzce	41°05'N	31°07'E	3
A. flavicollis	Samsun	41°22'N	36°12'E	6
A. flavicollis	Ordu	40°47'N	37°00'E	10
A. flavicollis	Giresun	41°00'N	38°48'E	14
A. flavicollis	Trabzon	40°49'N	39°37'E	6
A. flavicollis	Rize	40°46'N	40°33'E	21
A. flavicollis	Artvin	41°07'N	42°03'E	24
A. mystacinus	Zonguldak	41°27'N	31°47'E	7
A. mystacinus	Düzce	41°05'N	31°07'E	6
A. mystacinus	Ordu	40°47'N	37°36'E	2
A. mystacinus	Trabzon	40°50'N	39°42'E	14
A. mystacinus	Rize	40°46'N	40°33'E	11
A. mystacinus	Artvin	41°21'N	41°40'E	24
A. witherbyi	Çanakkale	40°09'N	26°24'E	4
A. witherbyi	Istanbul	41°07'N	29°06'E	3
A. witherbyi	Kocaeli	40°42'N	30°05'E	4
A. witherbyi	Samsun	41°22'N	36°12'E	9
A. witherbyi	Ordu	40°52'N	37°45'E	1
A. witherbyi	Trabzon	40°54'N	40°06'E	4
A. witherbyi	Rize	41°04'N	40°48'E	17
A. witherbyi	Artvin	41°14'N	42°09'E	11
A. witherbyi	Ardahan	41°30'N	42°43'E	5
Total				338

Results

In this study, based on the size of the first upper molar (UM1), it was observed that there was a variation among species. While *A. mystacinus* exceeded 15 units on the *y* axis and had the highest UM1 size, *A. uralensis* had the least UM1 size in the genus with its value close to 13.5 units. *Apodemus sylvaticus* and *A. flavicollis*, hardly mentioned in the literature due to many similar characteristics of their morphological distinctions, were the closest species of *Sylvaemus* in this size-based analysis (Fig. 4). However, it has to be noted that this graphic represent all the populations occurring in the north of Turkey (Fig. 1). When *A. sylvaticus*, *A. flavicollis*, *A. mystacinus* and *A. witherbyi* were analysed based on their sizes within their own species, they tended to display smaller body sizes towards the east but no considerable variation in size of *A. uralensis* was observed within the same geographic region (Helvaci 2012).

In the canonical analysis of all species of *Apodemus* ($P < 0.001$), Elliptic Fourier Transform (EFT) Outline Analysis graphic (Fig. 5) displayed a significant difference by pointing to values between +5 and +10 at the first axis (CA1= % 43.4) in the shape-based analysis (Classification matrix: 100% for *A. agrarius*, % 79 for all the species) of *A. agrarius* (the representative of the nominotypical subgenus of *Apodemus*). In the same analysis, *A. mystacinus* was partly differentiated at the second axis (CA2=26.5%) from the genus *Sylvaemus*, with its value reaching +5. Although there was not a clear distinction determined for *A. agrarius* (since this subgenus narrowed the distance in the group of *Sylvaemus*), samples of *A. uralensis* (Classification matrix: 92% for *A. uralensis*) exhibited their different molar morphology in the EFT analysis.

Discussion

The genus *Apodemus* has been broadly studied by using morphology and morphometrics to enlighten taxonomical problems and phenotypic variations for several decades (Niethammer 1969, Barciova & Macholán 2006, Jojić et al. 2014). Unlike other species of *Apodemus* occurring in Turkey, it is possible to identify *A. agrarius* only based on its upper molar characteristics due to the long elliptical shape of the first upper molar, the lack of t3 part in the second upper molar and the relatively small size of the third upper molar (in proportion to the other molars). In the outline analysis, *A. agrarius* differs from all other five studied species in terms of shape (Classification matrix: 100% for *A. agrarius,* 79%

for all other species). *Apodemus mystacinus* has a close relationship with the species of the subgenus *Sylvaemus* and also shows a very independent position within the genus in the present study. Quite similar relationships of *A. agrarius*, *A. mystacinus* and the species of *Sylvaemus* have been found by several studies using genetic approaches (e. g., Filippucci et al. 2002, Bellinvia 2004).

Morphological examinations and genetic analyses obviously discriminate *A. agrarius* from the species of *Sylvaemus* and *A. mystacinus*. As revealed by our analysis, this phylogenetic pattern fits well to the observed differentiation in the molar shape. The most divergent species of the genus *Apodemus*, i. e. *A. agrarius*, is also characterised by the most differentiated molar shape, whereas the species of the subgenus *Sylvaemus* (*A. uralensis*, *A. witherbyi*, *A. sylvaticus* and *A. flavicollis*) cluster close together in the morphospace. However, a few studies (Frynta et al. 2006, Çolak et al. 2007) define that *A. mystacinus* is more differentiated than *A. agrarius* and species of *Sylvaemus* based on traditional morphometrics. The traditional morphometric analysis is based on size and, since size (Fig. 4) and shape (Fig. 5) are separately evaluated in the outline analysis, *A. mystacinus* has a clearly bigger first upper molar as compared to the other species. Since *A. mystacinus* readily differs from other species of *Sylvaemus* in terms of shape morphology, it has been included within the subspecies of *Karstomys* (see Rietschel & Storch 1974, Storch 1975). However, several studies have rejected the validity of this subgenus (Corbet 1978, Niethammer 1978, Musser et al. 1996). *Apodemus mystacinus* is the biggest among all other species of *Apodemus* in Turkey; the first upper molar outline shape analysis shows that *A. mystacinus* is morphologically closer to the species of *Sylvaemus* but, based on the size analysis, it is away from them.

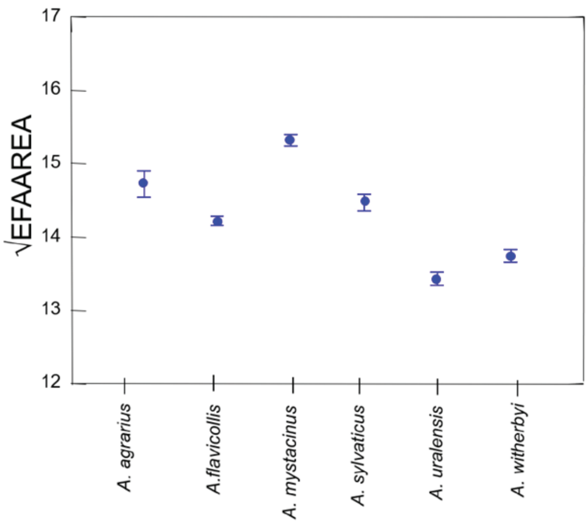

Fig. 4. Distribution of size among the species of *Apodemus* occurring in Turkey (first upper molar).

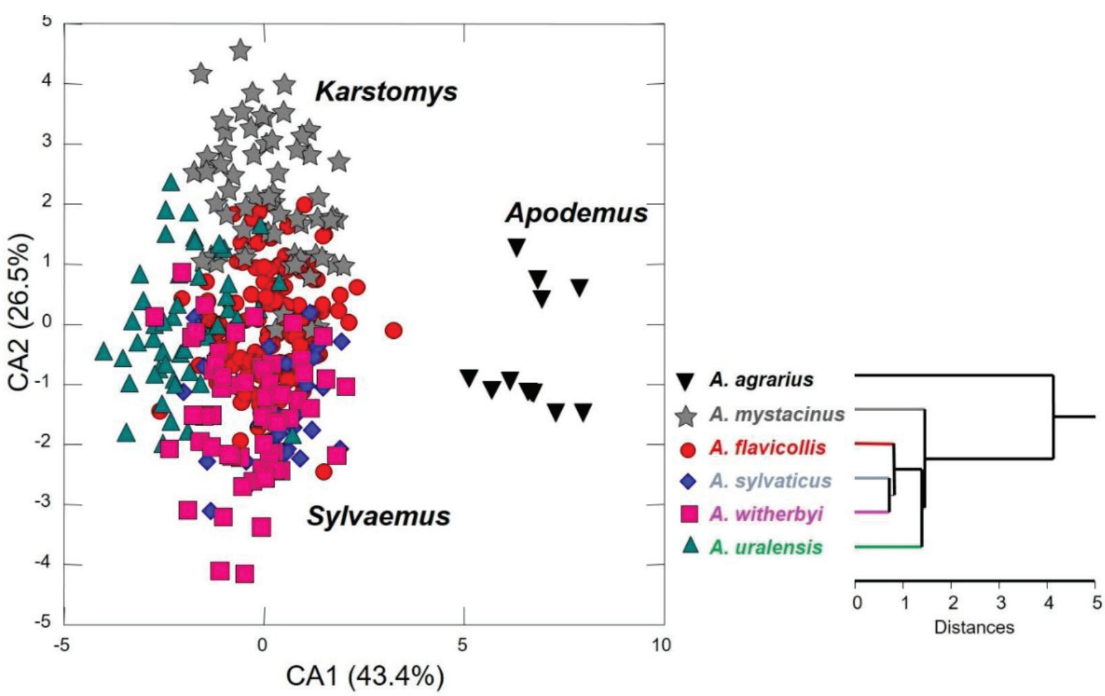

Fig. 5. Plot for shape variation of the first upper molar (UM1) within the six species of *Apodemus* in northern part of Turkey, displayed on the first two axes of a canonical analysis on the Fourier coefficients.

There are still debates on the position of *A. mystacinus* as a distinct subgenus (Filippucci et al. 2002, Michaux et al. 2002). In the present study, the first upper molar outline analysis does not identify a distinction between *Sylvaemus* and *Karstomys*. At the present level of knowledge of the group, it is difficult either to support the placement of *A. mystacinus* as a member of a distinct group (*Karstomys*) (Martin et al. 2000) or to include it in *Sylvaemus* (Filippucci et al. 2002, Michaux et al. 2002).

According to the outline analysis results, four species of the subgenus *Sylvaemus* are indisputably closely related (*A. sylvaticus, A. witherbyi, A. flavicollis* and *A. uralensis*). Within the scope of this study, it has been observed that close relatives in *Sylvaemus* exhibit overlapping characteristics. The fact that the molecular differentiation of the species that belong to the subgenus *Sylvaemus* is challenging due to the fact that its species are the youngest ones (Michaux et al. 2002). Outline morphometric analysis has shown once again that *Sylvaemus* is the youngest subgenus of *Apodemus* and includes recently differentiated species. Several studies have shown that one of the reasons making morphological differentiation between *A. flavicollis* and *A. sylvaticus* difficult is the variation of characters (Barciova & Macholán 2006). Considering all the characters (sutura coronalis, molar features, etc.) identified in the analysis, it is demonstrated that they are not constant in all samples. It has been noted that *A. sylvaticus* and *A. flavicollis* have one or many common characteristics in the localities where they sympatrically occur. Among species sharing a similar ecology, morphological differences have been shown to accumulate with time together with neutral genetic differentiation (Ledevin et al. 2012). Our results suggest that these two species are very close to one another in terms of shape and size as pointed out also by previous studies.

Compared to other species, the body size of *A. uralensis* is highly reduced (Fig. 6), and this might be a result of a selection directed to reducing total energy consumption more than in other species (Ledevin et al. 2010). This species, unlike others (e.g., *A. flavicollis*), is specific to its habitat and specialised in using limited resources. This well explains the allopatric distribution of *A. uralensis* in the region, whereas there are not many species in the Central Black Sea forests, which are seriously destroyed by human activities.

As a result, we consider the outline analysis as being highly explanatory in relation to many topics in the taxonomy of *Apodemus*. In addition to the morphometric analyses of the first upper molar, performing different morphometric methods (on skull and mandible) jointly would be quite informative for future studies on taxonomy of *Apodemus*.

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References

Barciova L. & Macholán M. 2006. Morphometric study of two species of wood mice *Apodemus sylvaticus* and *A. flavicollis* (Rodentia Muridae) traditional and geometric morphometric approach. Acta Theriologica 51: 15–27.

Bellinvia E. 2004. A phylogenetic study of the genus *Apodemus* by sequencing the mitochondrial DNA control region. Journal of Zoological Systematics and Evolutionary Research 42: 289–297.

Çolak R., Çolak E., Yiğit N., Kandemir I. & Sözen M. 2007. Morphometric and biochemical variation and the distribution of the genus *Apodemus* (Mammalia: Rodentia) In Turkey. Acta Zoologica Academiae Scientiarum Hungaricae 53: 239–256.

Corbet G. 1978. The mammals of the Palaearctic region: a taxonomic review. London: British Museum (Natural History).

Darvish J., Mohammadi Z., Ghorbani F. & Mostafavi E. 2014. Morphological morphometric characterisation of the eastern broad-toothed field mouse *Apodemus mystacinus* (Rodentia: Muridae) from Zagros Mountains, north-western Iran. Acta Zoologica Bulgarica 66 (4): 461–468.

Filippucci M. G., Macholán M. & Michaux J. R. 2002. Genetic variation and evolution in the genus *Apodemus* (Muridae: Rodentia). Biological Journal of the Linnean Society 75: 395–419.

Filippucci M. G., 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.

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: 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.

Ge D., Feijó A., Cheng J., Lu L., Liu R, Abramov A. V., Xia L., Wen Z., Zhang W., Shi L. & Yang Q. 2019. Evolutionary history of field mice (Murinae: *Apodemus*), with emphasis on morphological variation among species in China and description of a new species. Zoological Journal of the Linnean Society 187: 518–534.

Helvaci Z. 2012. Kuzey Anadolu ve Trakya'da Yayılış Gösteren *Apodemus* Kaup, 1829 (Mammalia: Rodentia) Cinsinin Morfolojik ve Morfometrik Analizi. Ankara University, Ankara.

Jojić V., Bugarski-Stanojević V., Blagojević J. & Vujošević M. 2014. Discrimination of the sibling species *Apodemus flavicollis* and *A. sylvaticus* (Rodentia, Muridae). Zoologischer Anzeiger 253: 261–269.

Krystufek B. & Vohralík V. 2007. Distribution of field mice (*Apodemus*) (Mammalia: Rodentia) in Anatolia. Zoology in the Middle East 42: 25–36.

Kryštufek B., Vohralík V. & Janžekovič F. 2009. Mammals of Turkey and Cyprus: Rodentia II: Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromydae, Hystricidae, Castoridae. Univerza na Primorskem, Znanstveno-raziskovalno središče, Založba Annales.

Ledevin R., Quere J. P., Michaux J. R. & Renaud S. 2012. Can tooth differentiation help to understand species coexistence? The case of wood mice in China. Journal of Zoological Systematics and Evolutionary Research 50: 315–327.

Ledevin R., Quere J. P. & Renaud S. 2010. Morphometrics as an insight into processes beyond tooth shape variation in a bank vole population. Plos One 5 (11): e15470.

MacLeod N. & Forey P. 2002. Morphometrics, shape, and phylogenetics. London: Taylor and Francis. pp. 100–138.

Martin Cerezo M. L., Kucka M., Zub K., Chan Y. F. & Bryk J. 2020. Population structure of *Apodemus flavicollis* and comparison to *Apodemus sylvaticus* in northern Poland based on RAD-seq. BMC Genomics 21 (1): 1–14.

Martin Y., Gerlach G., Schlotterer C. & Meyer A. 2000. Molecular phylogeny of European muroid rodents based on complete cytochrome b sequences. Molecular Phylogenetics and Evolution 16: 37–47.

Michaux J. R., Chevret P., Filippucci M.G. & Macholán M. 2002. Phylogeny of the genus *Apodemus* with a special emphasis on the subgenus *Sylvaemus* using the nuclear IRBP gene and two mitochondrial markers: cytochrome b and 12S rRNA. Molecular Phylogenetics and Evolution 23: 123–136.

Musser G., Brothers E., Carleton M. & Hutterer R. 1996. Taxonomy and distributional records of Oriental and European *Apodemus*, with a review of the *Apodemus*-*Sylvaemus* problem. Bonner Zoologische Beiträge 46: 143–190.

Musser G. G. & Carleton M. D. 1993. Family Muridae. In: Wilson D. E. & Reeder D. M. (Eds.): Mammal species of the World: A taxonomic and geographic reference. Washington and London Smithsonian Institute Press. pp. 501–755.

Musser G. G. & Carleton M. D. 2005. Family Muridae. In: Wilson D. E. & Reeder D. M. (Eds.): Mammal species of the World. A taxonomic and geographic reference. Baltimore: The Johns Hopkins University Press. pp. 894–1531.

Niethammer J. 1969. Zur Frage der Introgression bei den Waldmaüsen *Apodemus sylvaticus* and *A. flavicollis* (Mammalia, Rodentia). Zeitschrift für zoologische Systematik und Evolutionsforschung 7: 77–156.

Niethammer J. 1978. *Apodemus mystacinus* (Danford and Alston, 1877) – Felsenmaus. *Apodemus flavicollis* (Melchior, 1834) – Gelbhalsmaus. *Apodemus sylvaticus* (Linnaeus, 1758) – Waldmaus. In: Niethammer J. & Krapp F. (Eds.): Handbuch der Säugetiere Europas: Wiesbaden: Akademische Verlagsgesselschaft. pp. 306-358 pp.

Rietschel S. & Storch G. 1974. Außgewöhlich erhaltene Waldmäuse (*Apodemus atavus* Heller, 1936) aus dem ber-Pliozän von Willershausen am Harz. Senkenbergiana Lethaea 54: 491–519.

Serizawa K., Suzuki H. & Tsuchiya K. 2000. A phylogenetic view on species radiation in *Apodemus* inferred from variation of nuclear and mitochondrial genes. Biochemical Genetics 38: 27–40.

Storch G. 1975. Eine Mittelpleistozäne Nager-Fauna von der Insel Chios, **Ägäis** (Mammalia, Rodentia). Senkenbergiana Biologica 56 (4-6): 165–189.

Wilson D. E. & Reeder D. M. 2005. Mammal Species of the World. A Taxonomic and Geographic Reference. Baltimore: Johns Hopkins University Press. pp. 2-142.

Zelditch M. L., Swiderski D. L., Sheets H. D. & Fink W. L. 2004. Geometric morphometrics for biologists: a primer. New York: Elsevier Academic Press.

Zimmermann K. 1962. Die Untergattungen der Gattung *Apodemus* Kaup. Bonner Zoologische Beiträge 13: 198–208.

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