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Test of character displacement in urban populations of *Apodemus sylvaticus*

P. Mikulová and D. Frynta

Abstract: We studied the wood mouse, *Apodemus sylvaticus*, inhabiting parks, cemeteries, suburban woods, and other green areas in the city of Prague. To assess the character displacement and (or) release hypothesis we compared seven samples from local populations occurring sympatrically with *Apodemus flavicollis* with 10 samples from those localities in which *A. flavicollis* has never been recorded. The analysis included 1410 specimens of *A. sylvaticus* collected during the years 1980–1990. Seventeen skull and body characters were measured. Then the data were age- or size-adjusted and treated by principal-component analyses. Factor scores were further subjected to statistical testing. Although the results revealed considerable variation among localities, they did not suggest character displacement and (or) release. *Apodemus sylvaticus* from populations sympatric with *A. flavicollis* were morphometrically similar to their conspecifics from other populations collected at the periphery of the city. However, slight but statistically highly significant differences were found between samples from localities in the city centre and those from the periphery. This phenomenon may be interpreted as the effect of urbanisation or isolation by built-up areas.

Résumé : Nous avons étudié les populations d'*Apodemus sylvaticus* dans des parcs, des cimetières, des boisés de banlieue et d'autres zones vertes de la ville de Prague. Pour éprouver les hypothèses de glissement et d'expansion de niche, nous avons comparé sept échantillons prélevés à même les populations locales vivant en sympatrie avec *Apodemus flavicollis* à 10 échantillons prélevés à d'autres sites d'où *A. flavicollis* a toujours été absent. Le matériel contenant 1410 spécimens d'*A. sylvaticus* récoltés entre 1980–1990 a été analysé. Dix-sept caractères du corps et de la tête ont été mesurés. Les données ont ensuite été ajustées en fonction de l'âge ou de la taille pour être soumises à une analyse en composantes principales. Les positions sur les facteurs ont été soumises à d'autres tests statistiques. Bien que les résultats mettent en lumière une importante variation d'une localité à l'autre, ils n'indiquent ni glissement, ni expansion de niche. Les *A. sylvaticus* vivant en sympatrie avec des *A. flavicollis* sont morphologiquement semblables aux individus de la même espèce provenant d'autres populations recueillies en périphérie de la ville. Cependant, nous n'avons trouvé que des différences minimes, quoique hautement significatives, entre les échantillons prélevés en ville et ceux de la périphérie. Ce phénomène peut s'interpréter comme l'effet de l'urbanisation ou de l'isolement créé par la présence des agglomérations.

[Traduit par la Rédaction]

Introduction

Character displacement and (or) release is a widely applied concept in evolutionary ecology that is currently receiving increasing interest (Doebeli 1996; Case and Taper 2000; Day 2000). It predicts that selective forces accompanying interspecific competition between ecologically similar species in sympatry will cause evolutionary change in some characters, e.g., morphological traits (Brown and Wilson 1956; Grant 1972, etc.). The phenomenon of morphological differences between populations that occur in the presence and absence of a competitor has been repeatedly demonstrated in several vertebrate taxa such as lizards (Losos 1990; Giannasi et al. 2000), birds (Lack 1947; Fjeldsa 1983; Grant 1986), marsupials (Jones 1997), carnivores (Dayan et al. 1992), and shrews (Malmquist 1985). Surprisingly, few studies (e.g., Patterson 1981; Alcántara 1991; Yom-Tov 1991; Yom-Tov et al. 1999) have been devoted to rodents, although interspecific competition has been repeatedly demonstrated in this group (Schoener 1983; Abramsky 1984; Dueser et al. 1989).

Apodemus flavicollis Melchior, 1834 and *Apodemus sylvaticus* Linnaeus, 1758 are species that are widespread in Europe. Their ecology has been extensively studied (cf. Jüdes 1982; Montgomery 1989*a*; Wilson et al. 1993) and obviously can serve as a proper model for testing character displacement and (or) release (Alcántara 1991; cf. Dayan and Simberloff 1998). They are closely related to each other (cf. Bellinvia et al. 1999), they are morphologically similar (e.g., Tvrtkovic 1979), their distributions overlap considerably (Mitchell-Jones et al. 1999), and frequently they even share microhabitats (Montgomery 1980, 1981, 1989*b*). Moreover, only minor differences are found in their food niches (e.g., Hoffmeyer 1976; Holišová and Obrtel 1980; Obrtel and Holišová 1983; Heroldová 1994). Considering that the availability of food resources, especially seeds, is a key factor in population regulation for both species (Montgomery 1989*c*; Pucek et al. 1993), exploitation competition can reasonably be expected. There is also some evidence for interference

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competition. Behavioural studies carried out in the laboratory and (or) in enclosures have repeatedly proved strong dominance of *A. flavicollis* over *A. sylvaticus* (Hoffmeyer 1973; Montgomery 1978; Čiháková and Frynta 1996*a*). The loser can be expected to suffer from asymmetric interference competition even in natural conditions. So a character change resulting from competitive interaction is more likely to occur in *A. sylvaticus* than in *A. flavicollis*.

In spite of its similar biology, *A. flavicollis* exhibits greater spatial, aboveground, and vertical activity than *A. sylvaticus*; it is also a better climber, jumper, and fighter. Morphological studies have revealed that *A. flavicollis* is larger and heavier and possesses bigger molars, longer hind feet, and a relatively longer tail than *A. sylvaticus*. Most of these differences can be easily attributed to the size difference. Without doubt, size causally correlates with many aspects of performance, such as fighting ability, food consumption, and foraging and processing efficiency with respect to seeds of different sizes. Therefore, we expect that the putative character displacement primarily affects the overall size of the animal, which can be easily expressed as, for example, the first principal component extracted from numerous skull and body measurements. However, particular characters related to a specific function (e.g., hind-foot and tail length with respect to locomotion and climbing, dental measurements with respect to chewing) may also be a target of selection, resulting in a change in shape.

We studied morphometric traits in *A. sylvaticus* collected in parks, cemeteries, suburban woods, and other green areas in Prague. We took advantage of the fact that Prague is one of the most extensively studied cities in terms of small-mammal communities, consequently an adequate number of museum specimens was available. From the 1960s to the 1990s about 12 000 specimens were collected in more than 100 localities distributed in the area of the city (Frynta et al. 1994; Čiháková and Frynta 1996*b*). So the distribution pattern of *Apodemus* species in Prague is well documented. While *A. sylvaticus* is widespread and dominant in most localities, *A. flavicollis* is confined to a few suburban woods, where it is usually well represented. In these localities the two species occur in close sympatry. In the other localities *A. flavicollis* is absent in spite of the widespread availability of suitable habitats (cf. Frynta et al. 1994). This phenomenon is attributable to immigration/extinction rates resulting from habitat fragmentation and (or) isolation of individual green areas by built-up areas. The above-described distribution pattern of *Apodemus* species enables us to study character displacement on a very fine scale, i.e., within a set of populations closely associated in time, space, and ancestry. However, it was necessary to control our comparisons for the effect of urbanisation itself, which has been repeatedly demonstrated to influence the ecology and morphology of rodent populations in large cities (e.g., Andrzejewski et al. 1978; Gliwicz 1980).

There is some indirect evidence of competition between *Apodemus* species in Prague. In localities where *A. flavicollis* is absent, *A. sylvaticus* occupies the forest habitats typical of the former species and reaches high numbers there. Moreover, male *A. flavicollis* captured in Prague populations were highly aggressive when tested in a small enclosure. They immediately approached, attacked, and even killed not only conspecific males but also every *A. sylvaticus* (Čiháková and Frynta 1996*a*; unpublished data).

The aims of this study were (*i*) to assess morphometric differentiation among individual populations of *A. sylvaticus* in Prague, (*ii*) to compare *A. sylvaticus* from localities where its competitor, *A. flavicollis*, was present and absent, (*iii*) to discuss the character displacement and (or) release hypothesis, and (*iv*) to evaluate the effects of isolation and (or) urbanisation on morphometric traits.

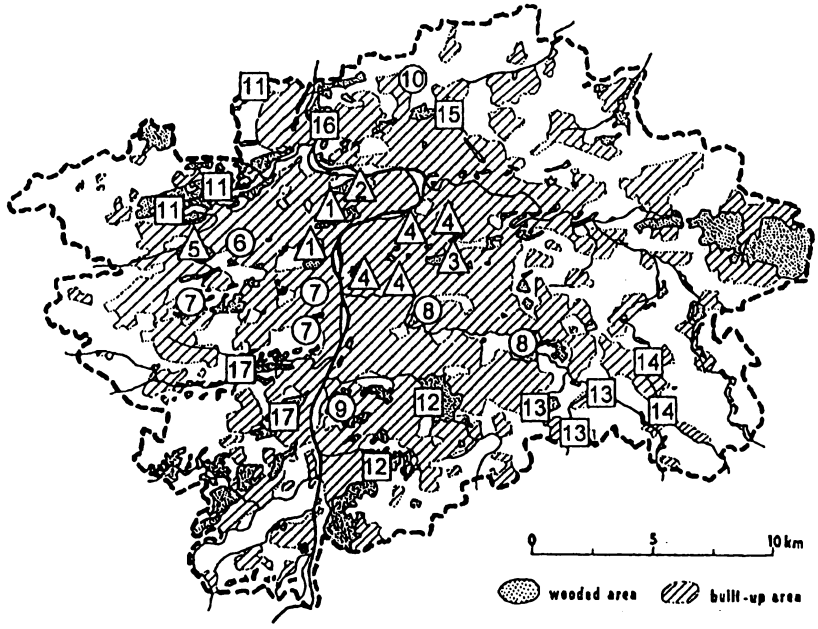
Material and methods

We used 1410 *A. sylvaticus* snap-trapped during the years 1980–1990 in the Prague area. After capture, standard external measurements were taken with callipers to the nearest 1 mm (body length (LC), tail length (LCD)) or 0.1 mm (ear length (LAU) and hind-foot length (LTP). Each individual was sexed, weighed to the nearest gram (the cube root of body mass (WRED) was used; for pregnant females the mass of embryos was subtracted) and dissected. Later, the skulls were removed and biologically prepared using *Dermestes* beetles. A further 10 cranial measurements were taken with callipers to the nearest 0.1 mm (the first 8 measurements) or a stereomicroscope to the nearest 0.05 mm (FIL, FIR; see below): condylobasal length (CBL; the distance from the prosthion to the condylion), facial length (FL; the distance from the prosthion to the straight line connecting the aboral edges of the M^3 crowns), rostral width (RW; maximum rostral width measured just in front of the zygomatic bones), interorbital width (IOW; minimum distance), brain-case width (BCW; measured just behind the zygomatic bones), interbullar width (IBW; the shortest distance between the left porus acusticus externus and the right one), rostral height (RH; the shortest rostral height just behind the incisors), brain-case height (BCH; taken in the region of the bullae tympanicae), the length of foramen incisivum on the left and right side, respectively (FIL and FIR). Six dental measurements (measured on the crowns as maximum distances) were taken under the stereomicroscope: the length (to the nearest 0.025 mm) of the upper molar row on the left and right side, respectively (UML and UMR), the length of the first upper molar on the left and right side, respectively (LM1L and LM1R), the width (to the nearest 0.014 mm) of the first upper molar on the left and right side, respectively (WM1L and WM1R). Molar abrasion was assessed under the stereomicroscope. We used 7 categories of abrasion that corresponded to the 6-category classification described by Steiner (1968) with the second category split in two to obtain a finer scale.

The populations of *A. sylvaticus* in Prague, unlike those in some other areas, are easily distinguishable from sympatric *A. flavicollis*. Species identifications made according to external characters and coloration were subsequently verified by examining tooth measurements and plotting the length of the foramen incisivum against facial length as suggested by Tvrtković (1979).

The studied specimens came from 33 localities. To avoid using samples consisting of only a few individuals, we pooled some samples in view of the close geographical proximity and similar habitat types and distribution of *A. flavicollis*. The resulting number of samples, hereinafter referred as localities, was only 17 (Fig. 1). Names used for localities, sample sizes, and grouping of original samples are as follows (numbers in parentheses are original locality numbers; for details see Frynta et al. 1994): (1) Petřín (88, 91, 92, 94), n = 106; (2) Stromovka (96), n = 340; (3) Nový židovský hřbitov (47), n = 135; (4) Vítkov (44, 48, 49, 54), n = 60; (5) Hvězda (84), n = 210; (6) Markéta (85, 86), n = 45; (7) Malvazinky (78, 79, 82), n = 64; (8) Hostivař (40, 43), n = 70; (9) Hodkovičky (63), n = 31; (10) Chabry (12), n = 58; (11) Šárka (101, 102,104), n = 52; (12) Kunratický les (38, 66), n = 38; (13) Průhonice (30, 32, 34), n = 43; (14) Uhříněves (26, 28), n = 58;

Fig. 1. Map of Prague showing the locations of the study sites (triangles denote "centre," circles denote "periphery," and squares denote "sympatry"; see the text). Locality numbers refer to samples described in Material and methods.



(15) Ďáblický hřbitov (13), n = 33; (16) Podhoří (3), n = 30; (17) Prokopské údolí (60, 72), n = 37.

The localities were assigned to three zones: (1) centre (localities 1–5): city parks or cemeteries well isolated by built-up areas, except one (locality 5); they were right in the centre of the city; (2) periphery (localities 6–10): less isolated green areas (shrubs (localities 6–8), woods (locality 9), ruderal sites (locality 10)) outside the city centre; (3) sympatry: all localities where *A. flavicollis* occurs sympatrically, i.e., woods and parks at the periphery of Prague (localities 11–17). The relative proportions of *A. flavicollis* in the samples collected in localities where *A. flavicollis* and *A. sylvaticus* occur sympatrically were as follows: 15.2% (n = 217) in locality 11, 7.9% (n = 378) in locality 12, 39.8% (n = 395) in locality 13, 64.5% (n = 166) in locality 14, 10.9% (n = 101) in locality 15, 8.8% (n = 34) in locality 16, and 8.3% (n = 204) in locality 17. However, most trap lines were laid in ecotones, i.e., the typical habitat of *A. sylvaticus*, therefore the proportion of *A. flavicollis* is somewhat underestimated. In another typical suburban forest at the periphery of Prague for which long-term census data are available, the ratio between these species was approximately balanced (Čiháková and Frynta 1996*b*).

For the purpose of eliminating geographical affinities we divided localities into five "local" groups, each consisting of three or four localities in one geographical direction from the city centre and including one or two localities in each zone (northwest 5, 6, 11; south-southwest 1, 7, 17; south-southeast 4, 9, 12; southeast 3, 8, 13, 14; north-northeast 2, 10, 15, 16).

Postnatal growth continues throughout life in *A. sylvaticus* (Frynta and Žižková 1992) Statistical correction for the age and (or) size of studied animals is therefore a crucial step in any morphometric analysis. We used molar abrasion as an age estimator and FL as an estimator of size. FL was selected because of its rapid rate of postnatal increase compared with the other cranial measurements (cf. Frynta and Žižková 1992).

To remove the effect of age, for each measurement we calculated residuals from an ANOVA model. The model included molar abrasion and in some measurements (WRED, LC, LCD, LTP) also sex and interactions as factors. Tooth measurements showing no postnatal growth were processed because they may be affected by abrasion itself. Similarly, to obtain size-corrected values, the data were log-transformed and the residuals from linear regression on FL were calculated for each measurement except tooth measurements, which were further treated as a raw data (there was no need for size correction). The above calculations were performed using Statgraphics version 5.0, while Statistica 4.5 was used for most calculations reported below.

One-way ANOVA procedures were performed on both age- and size-adjusted data to confirm that mice captured in individual localities vary in their morphometric traits. They revealed that the factor locality was highly significant ($p < 0.005$) in most measurements (except age-adjusted LC, IOW, WM1L, and WM1R and size-adjusted LTP, CBL, BCH, IBW, IOW, WM1L, and WM1R). The results became even more significant when the first three principal-component scores (PC1, PC2, and PC3) computed from age- or size-corrected data (see below) were considered (all $p \ll 0.0001$).

Both age- and size-adjusted data sets were further processed using the two following alternative methods: (1) Principal-component analysis (PCA) was performed on the whole data set consisting of 1410 individuals and 21 respectively 20 measurements. Mean values were used where measurements were missing. PC1, PC2, and PC3 extracted for each individual were subsequently compared by ANOVA in which the factors direction, zone, sex, and their interactions were evaluated. Tukey's tests (for unequal sample sizes) were performed to compare individual factor levels. (2) Median values were computed for each locality and measurement. The median was selected to avoid possible measurement errors, possible incorrect species identifications in sympatric localities, and (or) overrepresentation of localities from which a large amount of material was available. Then the PCA based on median values in 17 localities and 21 measurements was performed. PC1, PC2, and PC3 were extracted and their scores in individual localities further com-

Table 1. Principal-component loadings for sets of age- and size-adjusted data.

	Age-adjusted		Size-adjusted		
Trait	PC1	PC3	PC1	PC2	PC3
CBL	0.774	–0.181	0.358	–0.583	0.036
FL	0.863	–0.035			
FIR	0.652	0.106	0.292	–0.087	0.813
FIL	0.658	0.108	0.294	–0.070	0.815
RW	0.551	–0.114	0.069	–0.443	–0.177
IOW	0.475	–0.370	0.120	–0.354	–0.239
BCW	0.608	–0.426	0.073	–0.390	–0.395
IBW	0.634	–0.399	0.045	–0.416	–0.276
RH	0.714	–0.114	0.216	–0.388	–0.153
BCH	0.560	–0.382	0.064	–0.441	–0.250
UMR	0.584	–0.052	–0.874	–0.073	0.079
UML	0.582	–0.056	–0.879	–0.075	0.076
LM1R	0.462	–0.086	–0.839	–0.175	0.065
LM1L	0.459	–0.108	–0.834	–0.165	0.050
WM1R	0.358	0.149	–0.640	–0.301	0.236
WM1L	0.369	0.152	–0.609	–0.338	0.206
LC	0.696	0.345	0.294	–0.426	0.177
LCD	0.647	0.373	0.103	–0.549	0.133
LTP	0.600	0.316	–0.218	–0.258	–0.012
LAU	0.390	0.468	0.050	–0.279	0.116
WRED	0.610	0.435	0.368	–0.505	0.205
Variance explained	7.483	1.543	4.376	2.499	1.956
Proportion of total variance	0.356	0.073	0.219	0.125	0.098

Note: Individual measurements from each of 1410 specimens were considered in the PCA. See the text for an explanation of the abbreviations used for traits.

pared among the three zones by means of nonparametric statistics (Bonferroni-adjusted Mann–Whitney U test).

As a control we also performed a discriminant-function analysis in which raw measurements of all 21 variables were included as data and zone as a classification factor. This procedure allowed us to avoid data adjustment, as in the PCA method.

In addition, we compared matrices of morphometric similarity between localities (Euclidean distance based on median values) computed independently from the age- and size-adjusted data. We found good correspondence between them (approximate Mantel test, $t = 3.55$, $r = 0.56$, $p = 0.0020$). To verify the statistical independence of individual samples we compared the above morphometric matrices with the matrix of geographical distances between localities. No significant relationship was found by Mantel tests (NTSYS version 1.80).

Results

Age-adjusted data

PC1, PC2, and PC3 extracted from age-adjusted data explained 37, 16, and 7% of total variance, respectively (for factor loadings see Table 1). Factor scores computed for each specimen were further treated with ANOVA in which zone, local group, and sex were given as factors. The effect of zone (see Fig. 2) was apparent in both PC1 ($F = 22.6$, $p \ll 0.0001$, $R^2 = 2.94\%$) and PC3 ($F = 34.8$, $p \ll 0.0001$, $R^2 = 4.43\%$). It was not only highly significant but also exceeded the contribution of other factors: sex (PC1: $F = 6.0$, $p = 0.0144$; PC3: $F = 18.0$, $p < 0.0001$) and the zone – local group interaction (PC1: $F = 9.2$, $p \ll 0.0001$; PC3: $F = 2.9$, $p = 0.0029$). Tukey's post-hoc comparisons between individual zones revealed that centre differs both from periphery and sympatry (Tukey's test: $p < 0.0001$ for PC1 and PC3), the latter two zones exhibiting no difference from each other (PC1: $p = 0.8792$; PC3: $p = 0.3274$). We found no effect of zone on PC2; it was affected only by sex ($F = 15.0$, $p = 0.000$), local group ($F = 7.4$, $p < 0.0001$), and the zone – local group interaction ($F = 3.2$, $p = 0.0015$).

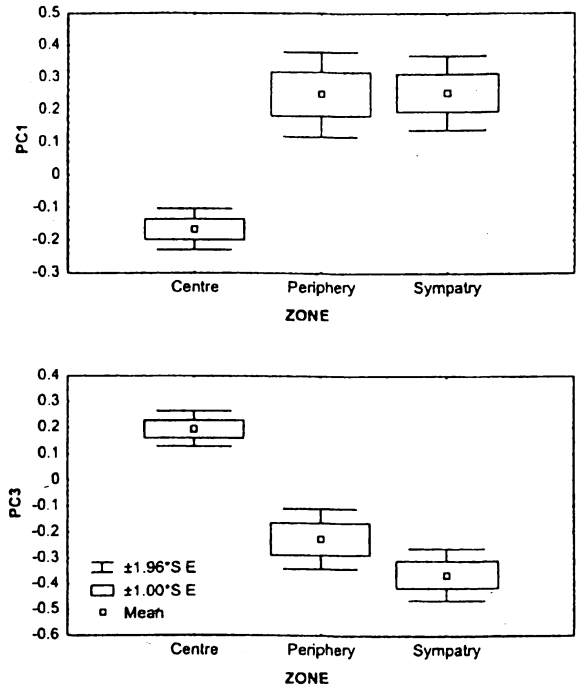
The above results were clearly supported when the original age-adjusted measurements rather than the principal-component scores were treated by the same ANOVA procedure. Mice from the centre differed (mostly they were smaller, though their body mass was greater, Tukey's test, $p < 0.05$) from those collected at the periphery and in sympatry in all variables except LAU, WM1L (centre > sympatry), RW (centre < periphery), and LC, LCD, and WM1R (no significant difference). We found no significant difference between periphery and sympatry by means of this procedure.

PC1, PC2, and PC3 computed from median values explained 42, 18, and 10% of the total variance. The difference between the localities situated in the centre and those at the periphery ($z = -2.40$, $p = 0.0487$) and in sympatry ($z = -2.52$, $p = 0.0354$) was supported when PC1 scores were compared. Another significant comparison was found between centre and sympatry in PC3 ($z = -2.68$, $p = 0.0222$). The partial separation of samples from centre localities from the other samples is visible from the PC1 versus PC3 plot (Fig. 3).

Size-adjusted data

Size-adjusted data produced comparable results. PC1, PC2, and PC3 explained 22, 12, and 10% of total variance, respectively (for factor loadings see Table 1). ANOVA (fac-

Fig. 2. Box plots of principal-component scores computed for each specimen from age-adjusted data and categorised according to zone.

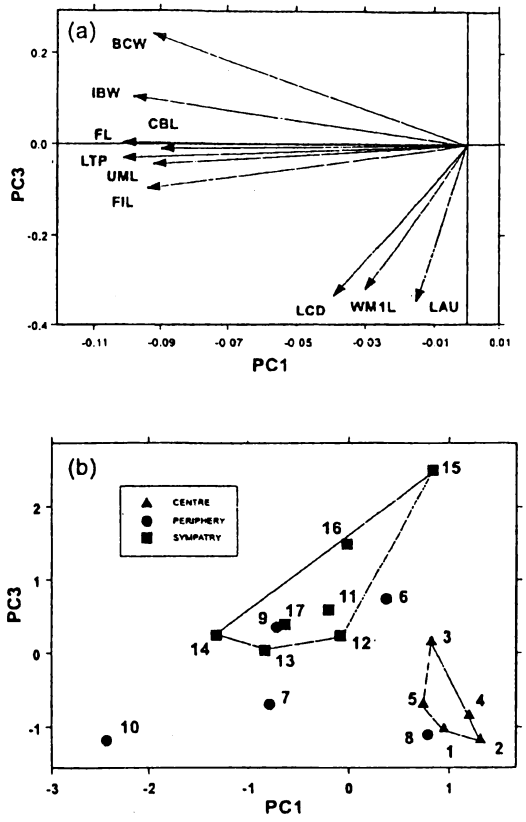


tors zone, local group, sex) revealed a significant effect of zone on PC1 (F = 18.3, p « 0.0001, R^2 = 2.43%), PC2 (F = 13.2, p « 0.0001, R^2 = 1.76%), and PC3 (F = 15.8, p « 0.0001, R^2 = 2.08%). Centre differed from periphery (Tukey's test, p = 0.0003 and p < 0.0187) and sympatry (Tukey's test, both p < 0.0001) in PC1 and PC3, respectively. PC2 scores for centre differed from those in sympatry (p < 0.0001), and in contrast to the other components, the difference between periphery and sympatry was also marginally significant (Tukey's test, p = 0.0221; see Fig. 4). The scores for each component were also influenced by the local group (PC1: F = 6.8, p < 0.0001; PC2: F = 5.9, p < 0.0001; PC3: F = 8.3, p « 0.0001) and the zone – local group interaction (PC1: 5.7, p « 0.0001; PC2: 3.0, p = 0.0027; PC3: F = 3.8, p = 0.0002) and PC2 also by sex (11.3, p = 0.0008).

When the original size-adjusted measurements were treated by the same ANOVA procedure, we found many significant differences (Tukey's test, p < 0.05) between centre and periphery (the former showing lower (BCW, LM1L, LM1R, UML, UMR) or higher (LAU, LC, WRED, LCD) values), as well as between centre and sympatry (the former showing smaller (BCW, LM1L, LM1R, UML, UMR) or higher (CBL, RW, FIL, FIR, LC, LAU, LCD, WRED) values), while only 2 of the 20 variables (LCD, RH) exhibited a significant difference between periphery and sympatry (the former showing higher values).

PC1, PC2, and PC3 computed from median values of size-adjusted data explained 31, 16, and 15% of total variance. The difference between centre and sympatry in PC1 (z = –2.46, p = 0.0421) was the only significant one; nevertheless, the mean score for periphery fits well that of sympatry (Fig. 5).

Fig. 3. (*a*) Factor scores (only loadings greater than 0.78 in PC1 and 0.6 in PC3 were considered). (*b*) Scatter plot of principal-component scores computed for each locality from median values of age-adjusted data. Numbers refer to localities/samples.



Discriminant-function analysis performed on raw data fully supported the above results obtained by means of PCA-based procedures: while the differences between centre and (or) periphery versus sympatry were highly significant (p « 0.0001), no differences were found between periphery and sympatry (p = 0.1178, ns).

Discussion

In spite of reasonable expectations, we found no clear evidence for character displacement and (or) release in *A. sylvaticus*. Although there was considerable morphometric variation between samples collected in different localities, no convincing difference was detected between periphery and sympatry. This finding may contribute to the current discussion concerning the role of character displacement. The absence of character displacement and (or) release in our results supports the more recent view that these phenomena were uncritically considered to be widespread (cf. Dayan and Simberloff 1998). Empirical support for their occurrence is weaker than is often believed, and is based on very small number of studies; in mammals, for example,

Fig. 4. Box plots of principal-component scores (PC1, PC2, and PC3) computed for each specimen from size-adjusted data and categorised according to zone.

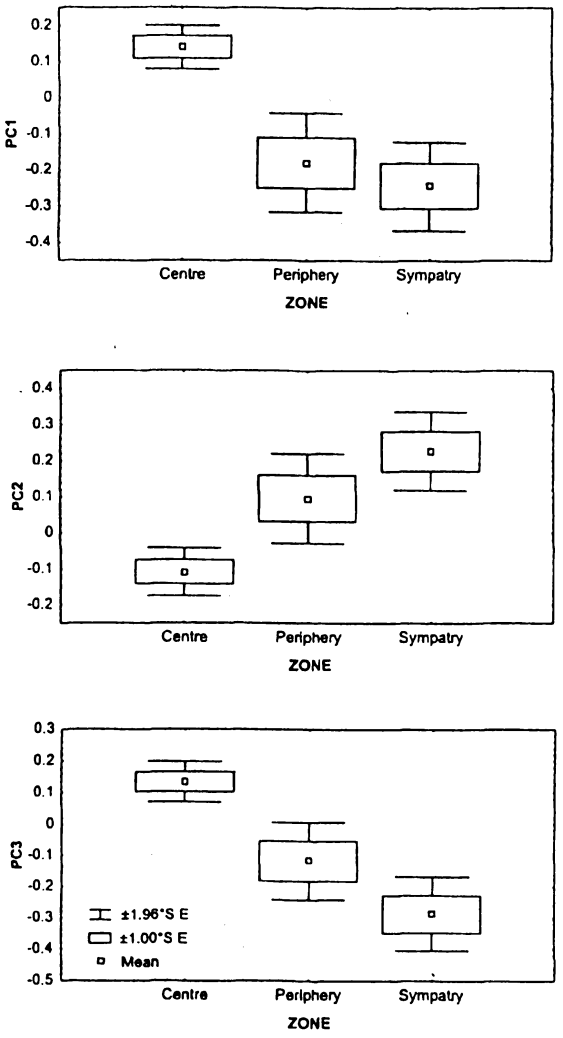
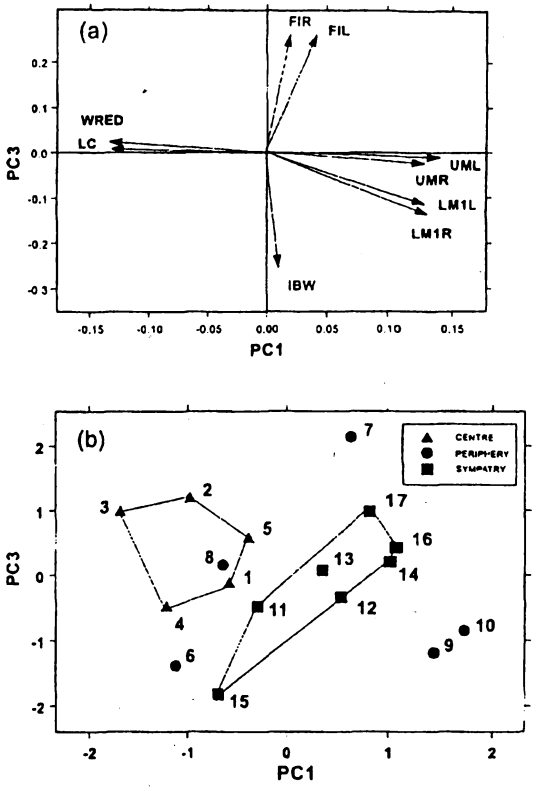


Fig. 5. (*a*) Factor scores (only loadings greater than 0.6 were considered). (*b*) Scatter plot of principal-component scores computed for each locality from median values of size-adjusted data. Numbers refer to localities/samples.



most were carried out on carnivores (Dayan and Simberloff 1998). On theoretical grounds it was argued that character displacement would not occur under many conditions when it might be expected, i.e., when the main requirements are met. Interspecific competition does indeed select for differences between species in the distribution of a trait, but under many circumstances intraspecific competition has the opposite effect and prevents displacement (Slatkin 1980; but see Doebeli 1996). Moreover, in some circumstances, not divergence but convergence of sympatric species (Abrams 1996) is to be expected.

Our interpretation of the results can be challenged by the argument that there was insufficient time or isolation for evolutionary change to occur. In Prague the rapid growth of built-up areas started in the second half of the 19th century and continued throughout the 20th century. Therefore, most parks (or suburban woods) have been isolated for at least several decades. There is a good evidence that rodent populations are able to undergo morphological changes over just a few generations (Berry 1964; Pizzimenti 1981; Pergams and Ashley 1999). However, gene flow may outweigh the selective forces operating on a local scale. Although we demonstrated morphometric differences between localities, their genetic nature is likely but uncertain.

Wood mice are not the only animals that exploit seed crops. There are also finches (*Fringilla coelebs*), which are widespread throughout the studied area in comparable densities (0.6, 1.1, 2.1, 1.8, and 0.5 pairs/ha in localities 1, 2, 3, 4, and 12, respectively; breeding-density estimates obtained by mapping singing males are available (R. Fuchs, personal observation in a letter), and bank voles (*Clethrionomys glareolus*), which are present in localities 5 and 9–17 (Frynta et al. 1994). However, these animals regularly switch from seeds to alternative food sources. This is especially important in spring, i.e., during the critical period for wood mouse populations, when seeds are scarce. As expected, the distribution pattern of neither finches nor bank voles is a good predictor of observed morphological change. The densities of other specialised seed-eating passerines (*Coccothraustes coccothraustes*, *Carduelis carduelis*, *Carduelis chloris*, *Serinus serinus*) are about 10 times lower (0.2, 0.4, 0.0, 1.5, and

0.2 pairs/ha in localities 1, 2, 3, 4, and 12, respectively; R. Fuchs, personal observation in a letter) than the normal density of *A. sylvaticus*. Not only low densities but also an inability to exploit seeds cached by wood mice (during the autumn period of high seed abundance) suggest that specialised seed-eating passerines are not likely candidates as competitors of wood mice.

There was a good agreement between the results obtained by means of different statistical models showing that wood mouse populations in the centre differed from those at the periphery and in sympatry. Mice from the centre tended to have slightly smaller skull and tooth measurements. These differences are small but statistically highly significant, and may be used as indirect evidence that our analysis was powerful enough to demonstrate even fine effects on morphometric traits.

It is not surprising that mice inhabiting the city centre differ somewhat from their conspecifics living in less urbanised areas. Similar effects on the population ecology (Andrzejewski et al. 1978; Gliwicz 1980; Babinska-Werka et al. 1981) and even morphology (Sikorski 1982*a*, 1982*b*; Liro 1988) of a related species, *Apodemus agrarius*, have been previously reported in Polish cities. However, our earlier attempts failed to demonstrate clear effects of the urbanisation gradient on the reproduction (Frynta 1992; Frynta and Vohralík 1992, 1994) and population structure (Frynta 1993; Frynta and Žižková 1994) of *A. sylvaticus* in Prague. Therefore, we can only speculate about the immediate cause of the morphometric change described in this study. Moreover, mouse populations inhabiting the city centre are influenced by highly correlated factors (e.g., isolation, climate change, predation, etc.), consequently it is difficult to falsify hypotheses concerning individual factors. Even the possibility that the observed effect is a product of character release cannot simply be excluded: the localities in the centre have been more protected from gene flow, their isolation has lasted longer, and *A. flavicollis* could even have been absent from there for longer.

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II.

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DISCRIMINANT ANALYSIS OF MORPHOMETRIC CHARACTERS IN FOUR SPECIES OF *APODEMUS* (MURIDAE: RODENTIA) FROM EASTERN TURKEY AND IRAN

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ABSTRACT

We studied 122 wood mice of the subgenus *Sylvaemus* that were collected from seven localities in Iran (the Zagros Mts. and the Caspian region), seven localities in eastern Turkey, and one locality in Armenia. After capture, mice were kept in captivity until reaching their adult size. The following species were determined using allozyme electrophoresis: *Apodemus uralensis* (= *microps*), *A. arianus* (= *hermonensis*), *A. flavicollis*, and a distinct form reported provisionally as *A.* cf. *hyrcanicus*. Body weight, four external measurements, and 22 dental and skull measurements were subjected to Discriminant Function Analysis in order to find morphometric criteria allowing species identification. Although there was a close similarity among studied species, 96%, 95%, and 95% of individuals were classified correctly when original measurements, log-transformed data, and residuals of the regression on condylobasal length ("size-out" procedure) were used, respectively. While *A. uralensis*, *A.* cf. *hyrcanicus*, and *A. arianus* were clearly separated from each other, *A. flavicollis* partly overlapped with *A. arianus*, as well as with *A.* cf. *hyrcanicus* in the morphometric space.

INTRODUCTION

Wood mice of the genus *Apodemus* are common rodents in the western part of the Palaearctic region (cf. Mitchell-Jones et al., 1999). Most of them belong to the subgenus *Sylvaemus* Ognev, 1924 (Musser et al., 1996), consisting of taxa which are closely related and morphologically similar to each other. For several decades there has been considerable research on the evaluation of morphological criteria enabling identification of traditionally recognized species, i.e., *A. sylvaticus* (Linnaeus, 1758), *A. flavicollis* (Melchior, 1834), and *A. microps* Kratochvíl and Rosický, 1952 (e.g., Amtmann, 1965; Haitlinger and Ruprecht, 1967; Steiner, 1968; Niethammer, 1969; Tvrtkovic, 1976, 1979; Ruprecht, 1978, 1979; Mezhzherin and Lashkova, 1992; Popov, 1993; Krystufek

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and Stojanovski, 1996). Recently, additional *Sylvaemus* species have been recognized in Asia and even in Europe (*A. alpicola* Heinrich, 1952 in the Alps—Storch and Lütt, 1989; Vogel et al., 1992). The picture has become complicated, especially in the territories of the former Soviet Union (e.g., Bulatova et al., 1991; Mezhzherin and Zykov, 1991; Orlov et al., 1996a,b; Mezhzherin, 1997a) and western Asia.

A. sylvaticus, which was previously believed to inhabit the entire territory of southern Russia and the Middle East, appeared to be absent from most of Eastern Europe (cf. Mezhzherin, 1997a) and also from southwestern Asia except for the westernmost part of Anatolia (Filippucci et al., 1996).

Wood mice populations from southern Russia and neighboring Central Asia seem to belong almost exclusively to the taxa *A. uralensis* (Pallas, 1811), *A. kastschenkoi* (Kuznetsov, 1932), and *A. pallipes* (Barret-Hamilton, 1900) (see also Mezhzherin and Mikhailenko, 1991; Mezhzherin, 1996; 1997a). *A. uralensis* is probably closely related to, or even conspecific with, European *A. microps*. Therefore, we follow the authors treating *A. microps* as a junior synonym of *A. uralensis* (e.g., Filippucci et al., 1996). While the evidence concerning the identity of *uralensis* and *microps* is based solely on allozyme electrophoresis, it was clearly demonstrated that populations from northern Anatolia were conspecific with European *A. microps* (breeding experiments—Steiner, 1979; allozymes—Filippucci et al., 1996; RAPD technique—Bellinvia et al., 1999).

The presence of another European species, *A. flavicollis* (= *A. tauricus* (Pallas, 1811) according to Mezhzherin, 1997a), was confirmed both in Israel (Filippucci et al., 1989; Filippucci, 1992) and in western Anatolia (Filippucci et al., 1996). Moreover, Steiner (1979) succesfully hybridized wood mice from eastern Turkey (district of Rize) with *A. flavicollis* from central Europe (Austria). In spite of this, Russian and Ukrainian authors, speculating on the basis of their results obtained in the Caucasus and the Transcaucasian region, suggested that the Middle East populations (including Asia Minor and Iran) should be included in a distinct species, *A. ponticus* Sviridenko, 1936 (Mezhzherin, 1991; Mezhzherin, 1997a).

One of the most important achievements of recent research on wood mice was the recognition of a new species in the Middle East. *A. hermonensis* Filippucci, Simson, and Nevo, 1989 was described in Israel (Filippucci et al., 1989; Filippucci, 1992), but was later found to be widespread, extending to western Anatolia (Filippucci et al., 1996) and even to Bozcaada Island in the Mediterranean Sea (Özkan and Kryštufek, 1999). As suggested by Filippucci et al. (1996), *A. hermonensis* is probably conspecific with the species reported as *A. falzfeini* Mezhzherin and Zagorodnyuk, 1989 or *A. fulvipectus* Ognev, 1824 (Mezhzherin and Zagorodnyuk, 1989) from Turkmenistan, the Transcaucasus, the Caucasus, and neighboring steppes up to Crimea. Recently, Mezhzherin (1997a) put *hermonensis, fulvipectus* (= *falzfeini*) into synonymy with *A. arianus* (Blanford, 1881) described from the Esfahan province in Iran. This view was supported also by Zagorodnyuk et al. (1997), and we follow it throughout this paper.

The last *Sylvaemus* species, *A. hyrcanicus* Vorontsov, Boyeskorov, Mezhzherin, Lyapunova, and Kandaurov, 1992, was described from the Hyrcanian Reserve in southeasternmost Azerbaijan (Mezhzherin, 1990; cf. Vorontsov et al., 1992).

Obviously, information concerning distribution and taxonomy of the *Sylvaemus* species in the extensive areas of eastern Asia Minor and Iran is scarce. Fortunately, a recent allozyme analysis (Macholán et al., 2001) confirmed the presence of *A. hermonensis* and *A. flavicollis* in both eastern Turkey and western Iran, *A. uralensis* in eastern Turkey, and a distinct species provisionally called *A.* cf. *hyrcanicus* in the Hyrcanian forests along the Caspian Sea in northern Iran. The aim of this study was to examine this biochemically identified material in order to find morphological criteria enabling the identification of these species in the Middle East. This is a necessary step before using museum collections as a source of data for studying the distribution and biology of a given species.

MATERIAL AND METHODS

The material was collected by the authors and other participants of the Czech biological expeditions to Armenia (1989), eastern Turkey (1995), and Iran (1996, 1997), and it is deposited in the collections of the Department of Zoology, Charles University in Prague. The localities are depicted in Fig. 1. The studied mice were mostly captured in the field (103 specimens) or they were of the first captive-born generation (19 specimens). All individuals were kept in captivity, usually for several months, in order to reach their asymptotic size. Consequently, most studied specimens can be considered as fully grown (see Frynta and Žižková, 1992, for the character of postnatal growth in *A. sylvaticus*). This procedure enabled us to rule out the effect of growth, while the size component of the variation remained unchanged. Altogether, we studied 122 specimens belonging to the following four species:

Apodemus uralensis 92: 27 specimens were collected in 6 localities in eastern Turkey (Seyfe 7, Güzyurdu 2, Yalnizcam Gecidi 1, Bagdasan 1, Damar 8, Kabaca 8).

Apodemus arianus 92: 48 specimens were collected in 11 localities in eastern Turkey (Seyfe 1, Güzyurdu 3, Bagdasan 4, Damar 1, Kabaca 1, Sirbasan 13); the Elbors Mts. (Vali Abad 1); and the Zagros Mts. (Gholaman 8, Yasuj 13, Abshar 2, Sivand 1) in Iran.

Apodemus flavicollis: 17 specimens were collected in 4 localities in Armenia (surroundings of Erevan 4); eastern Turkey (Güzyurdu 2, Kabaca 1); and the Zagros Mts. in Iran (Gholaman 10). Note: Some authors suggest that *flavicollis*-like populations from the neighboring Transcaucasus region belong to the distinct species *A. ponticus* (cf. Mezhzherin, 1997a). Having no evidence as yet concerning distinct differences in the biochemical characters between our populations and *A. flavicollis* from western Anatolia and/or Europe, we follow the conservative view.

Apodemus cf. *hyrcanicus*: 30 specimens come from two localities in the Hyrcanian forests along the Caspian Sea (Asalem 16, Now Kandeh 14). Note: *A. hyrcanicus* was described from the Hyrcanian Reserve in Azerbaijan (Vorontsov et al., 1992) some 80 km north of one of our sites in Asalem. Its conspecificity with our material from Iran is thus probable, but not certain (Macholán et al., 2001).

For the evaluation of geographic variation within species, we arbitrarily divided three well-represented species according to geographic criteria. *A. uralensis* were divided into

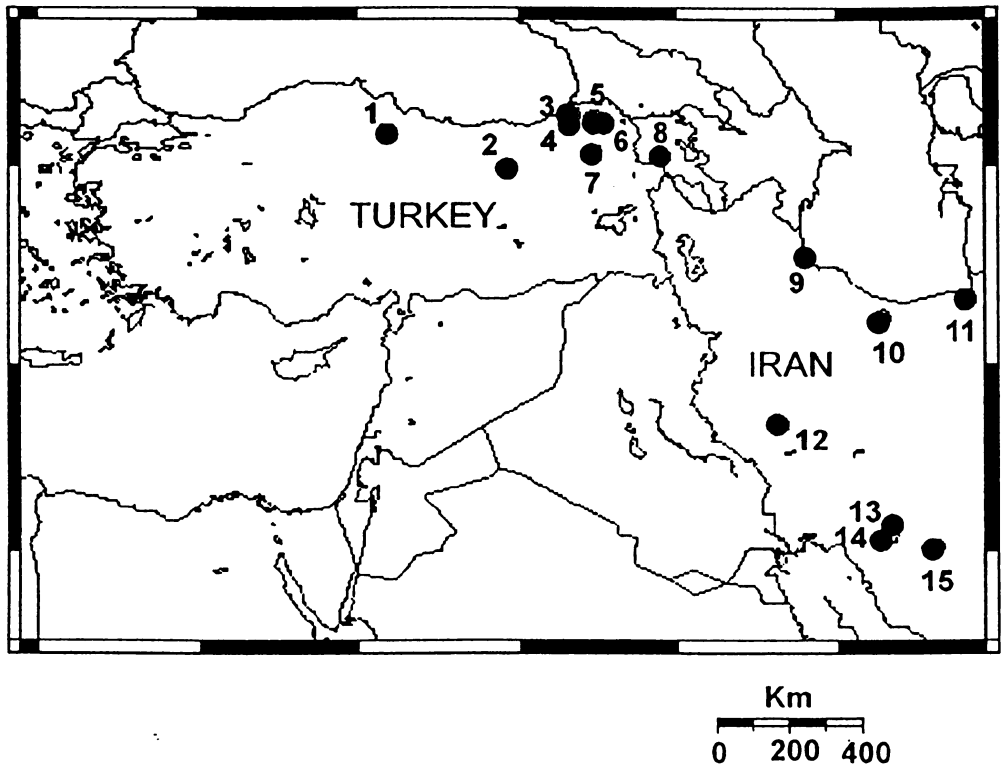

Fig. 1. Map of the localities studied. Explanations: (1) Seyfe, 35 km NNE of Amasya Province, ca. 1500 m. (2) Güzyurdu, 5 km S of Otlukbeli Mts., Gümüşhane Province, 2300 m, (3) Damar, 4 km SE of Murgul, S of Borçka, Artvin Province, ca. 2200 m. (4) Kabaca, 8 km S of Murgul, S of Borçka, Artvin Province, ca. 2000 m. (5) Yalnizcam Gecidi, Artvin Province, ca. 2000 m. (6) Bagdasan, Yalnizcam Mts., Kars Province, 2800 m. (7) Sirbasan, 5 km N, 25 km W of Sarikamiş, Güllü Mts., Kars Province, 2500 m. (8) Erevan, 10 km by road W of Echmiadzin, Armenia. (9) 12 km W of Asalem, Talesh Mts., Gilan Province, 280 m. (10) Vali Abad, Alborz Mts., Mazandaran Province, ca 2000 m. (11) Now Kandeh, 10 km S of Mazandaran Province, 200 m. (12) Gholaman, 30 km W of Khorram Abad, Zagros Mts., Lorestan Province, 1000 m. (13) Yasuj, 10 km N of Zagros Mts., Boyerahmad-va-Kuhgiluyeh Province, 2000 m, (14) Abshar, Zagros Mts., Fars Province, 1000 m. (15) Sivand, 10 km E of Zagros Mts., Fars Province, 1700 m.

western (localities Seyfe and Güzyurdu) and eastern (the other localities) samples, *A. arianus* into Turkish and Iranian samples, and *A.* cf. *hyrcanicus* into western (locality Asalem) and eastern (locality Now Kandeh) samples.

The specimens studied were either determined by biochemical methods (allozymes, 78 specimens, Macholán et al., 2001) or they were descendants of biochemically determined individuals (seven *A. flavicollis*: Erevan 4, and Gholaman 3; ten *A. arianus*: Yasuj 3, Sirbasan 7; two *A. uralensis*: Kabaca 2). An additional three individuals from Sirbasan were assigned to *A. arianus* because all nine biochemically determined individuals in this locality belong to this species. Similarly, 22 specimens from Asalem and

Now Kandeh were assigned to *A.* cf. *hyrcanicus* in accordance with eight biochemically determined specimens. These two localities concerned are characterized by wet woodland habitat, which is extremely uncommon in the Middle East. Moreover, the Hyrcanian forests along the Caspian coast have specific compositions of plant species. Therefore, the existence of one specialized wood mouse species, *A.* cf. *hyrcanicus,* is highly probable.

Each individual was sexed, weighed to the nearest gram (body weight—W), and dissected. Standard external measurements were taken with calipers to the nearest millimeter (body length—LC, tail length—LCD) or 0.1 mm (ear length—LA, and hind foot length—LTP). Later, the skulls were removed and biologically prepared using *Dermestes* larvae. A further 14 cranial measurements were taken with calipers to the nearest 0.1 mm (13 characters), or with a stereomicroscope to the nearest 0.05 mm (FI): CBL—condylobasal length, FL—facial length, PAL—palatal length, ZYG—zygomatic breadth, RW—rostral width (maximum distance), IOW—interorbital width (minimum distance), BCW—brain-case width, IBW—interbullar width (shortest distance between left and right porus acusticus externus), RH—rostral height, BCH—brain-case height, BULL—bulla length , FI—length of foramen incisivum, MZ, MU—width of choana (see Fig. 2). Eight teeth measurements (molars measured on the crowns as maximal distances) were taken with the use of a stereomicroscope: UML—upper molar row length (to the nearest 0.025 mm), M1L—first upper molar length, M1W—first upper

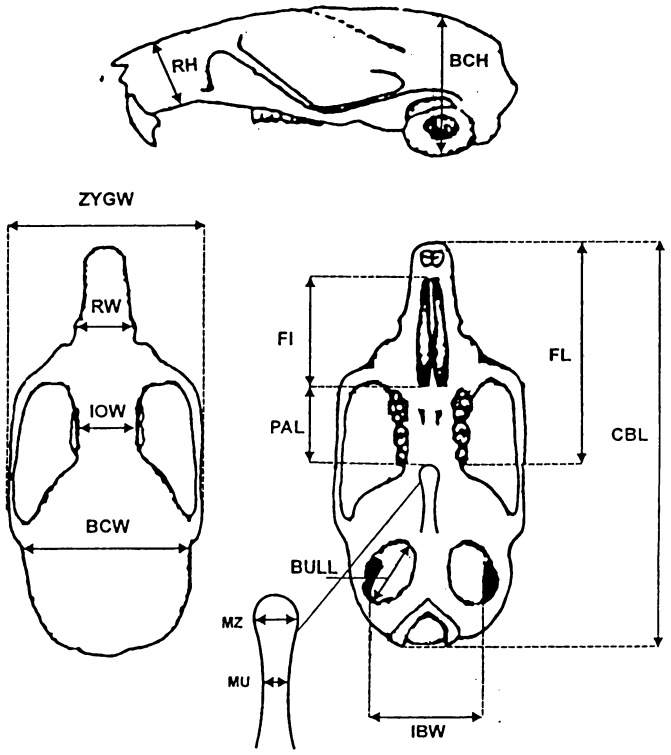

Fig. 2. 14 of the skull measurements studied (teeth measurements are not depicted). See Material and Methods for abbreviations.

molar width, M3L—third upper molar length, M3W—third upper molar width, LM1L—first lower molar length, LM1W—first lower molar width, INCW—upper incisor width (measured from the side view below os incisivum, to the nearest 0.014 mm). Molar abrasion according to Steiner (1968) was assessed using a stereomicroscope.

ANOVA/MANOVA and subsequent between-species post hoc comparisons by Tukey test for unequal N were applied for each measurement. Next, we performed Discriminant Function Analysis (DFA) and Canonical Analysis under the Discriminant Analysis subroutine of the STATISTICA Analysis System (release 4.0). Missing values of the raw data were replaced by those predicted from regression using condylobasal length as the independent variable. The data used were (1) original measurements, (2) log-transformed values, and (3) residuals from regression on condylobasal length (in measurements exhibiting postnatal growth) pooled with nontransformed measurements of molars. Residuals were used to rule out the effect of growth and size. This data set is further referred to as "size-out". Measurements of each data set and particular species were checked for normality prior to further analysis. Eight of 292 w-tests were highly significant ($p < 0.01$). They concerned two nontransformed (INCW in *A. arianus*, M3L in *A.* cf. *hyrcanicus*), three log-transformed (M3L and INCW in *A. arianus*, M3L in *A.* cf. *hyrcanicus*), and three size-adjusted variables (W, LCD, LA in *A.* cf. *hyrcanicus*). However, deviations from normality were small, inconsistent between species, and most distributions were both unimodal and symmetrical, as required for the multivariate procedures used.

To evaluate morphometric differences between species and/or populations, we computed Mahalanobis distances using Canonical Vector Analysis (CVA) based on pooled variance–covariance matrices (NTSYS version 1.80). UPGMA clustering was used to construct phenetic trees. Significance of morphometric distances was assessed by Hotelling tests (Marcus, 1993): $F = (n_1 + n_2 - p - 1) / ((n_1 + n_2 - 2) * p) * T^2$; $T^2 = D^2 * (n_1 * n_2) / (n_1 + n_2)$; $d.f._1 = n_1 + n_2 - p - 1$; $d.f._2 = p$; p = number of variables in matrix; n_1 and n_2 = sample sizes; D = Mahalanobis distance between samples.

We chose the data set consisting of original measurements, and applied the backward selection subroutine of DFA (F to remove was set to 4) to reduce the number of measurements. To derive classification functions suitable for practical use, we excluded the measurement suspected of having low interobserver reliability (MU) and performed the next run.

RESULTS

Descriptive statistics for particular species and the results of Tukey comparisons of means are given in Appendix 1. *A. uralensis* is obviously the smallest species: its mean values were found to be significantly smaller than in *A. hyrcanicus* (for all 27 variables), *A. flavicollis* (25 variables), and *A. arianus* (21 variables). *A. arianus* exhibited significantly lower mean values than *A.* cf. *hyrcanicus* and *A. flavicollis* in most variables (20 and 15, respectively). The latter two species differed in just six variables, *A.* cf. *hyrcanicus* exhibiting higher mean values in five of them. Results of the CVA and

subsequent cluster analysis (Fig. 3) showed that samples of each species cluster together. Hotelling tests revealed that none of the morphometrical distances between geographically defined samples belonging to a single species was significant. Surprisingly, the morphometric divergence between samples of *A. arianus* coming from geographically distant regions in Turkey and Iran is comparable to that between more proximate samples of *A. uralensis* or *A.* cf. *hyrcanicus*. Morphometric distances between samples belonging to different species were higher than the intraspecific ones, and some of them were significant (eastern sample of *A. uralensis* vs. *A. flavicollis* and *A.* cf. *hyrcanicus*; all comparisons concerning *A. arianus* except that with western sample of *A. uralensis*). All between-species comparisons became significant when samples belonging to each species were pooled prior to computing the Mahalanobis distances: *A. uralensis* vs. *A. arianus* ($D = 6.27$, $F = 16.2$, $p < 0.01$); *A. uralensis* vs. *A. flavicollis* ($D = 6.33$, $F = 5.89$, $p < 0.01$); *A. uralensis* vs. *A.* cf. *hyrcanicus* ($D = 5.75$, $F = 9.17$, $p < 0.01$); *A. arianus* vs. *A. flavicollis*, ($D = 3.95$, $F = 4.26$, $p < 0.01$); *A. arianus* vs. *A.* cf. *hyrcanicus* ($D = 4.83$, $F = 10.49$, $p < 0.01$); and *A. flavicollis* vs. *A. hyrcanicus* ($D = 3.71$, $F = 2.34$, $p < 0.05$). The above results suggesting the prevalence of between-species variation allowed us to introduce DFA for species as a classification factor.

Morphometric relationships among the studied species were visualized by projection into the first two canonical axes (see Table 1 for canonical variate loadings). Both "size-

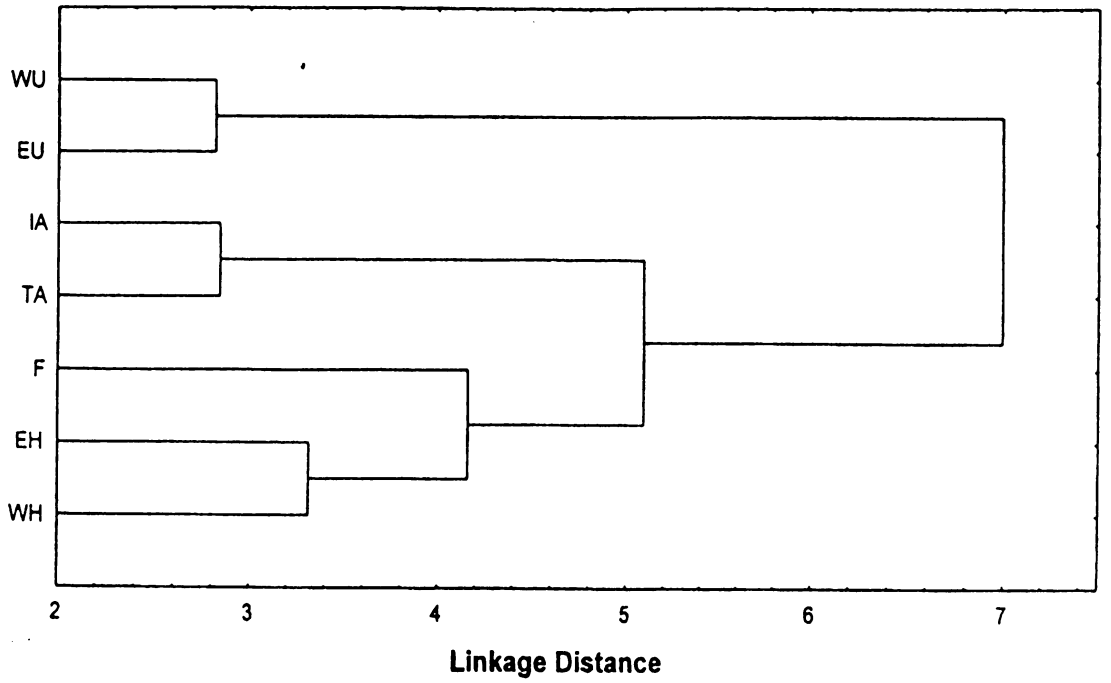

Fig. 3. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances. WU = western *A. uralensis*, EU = eastern *A. uralensis*, IA = Iranian *A. arianus*, TA = Turkish *A. arianus*, F = *A. flavicollis*, EH = eastern *A.* cf. *hyrcanicus*, WH = western *A.* cf. *hyrcanicus*.

in" (Fig. 4) and "size-out" (Fig. 5) procedures revealed that *A. uralensis* had the most separated position, and that the species *A. arianus* and *A.* cf. *hyrcanicus* were mutually distinct. *A. flavicollis* occupies an intermediate position between *A. arianus* and *A.* cf. *hyrcanicus*, partly overlapping these two species in morphometric space.

DFA was initially computed on the basis of all 27 variables. The classification was comparably successful when original measurements (ccc = 2.445, Wilk's $\lambda = 0.0155$, $R = 0.9256$, $\chi^2 = 439.35$, $F_{(81, 276)} = 10.30$, $p < 0.0001$), log-transformed values measurements (ccc = 2.489, Wilk's $\lambda = 0.0156$, $R = 0.9279$, $\chi^2 = 438.90$, $F_{(81, 276)} = 10.29$, $p < 0.0001$)

Table 1

Canonical variate loadings for 27 body, cranial, and teeth measurements. "Size-in" treatment = analysis based on original non-transformed measurements."Size-out" treatment = analysis based on residuals from regression on the condylobasal length (in measurements exhibiting postnatal growth) and non-transformed measurements of molars

Variable	"Size-in" analysis		"Size-out" analysis	
	CV1	CV2	CV1	CV2
W	0.170	0.087	–0.094	–0.117
LC	0.152	0.200	–0.036	–0.055
LCD	0.124	0.109	–0.033	–0.104
LTP	0.114	0.420	0.082	0.158
LA	0.196	0.245	–0.078	0.026
CBL	0.206	0.379	—	—
FL	0.108	0.459	0.218	0.238
FI	0.054	0.247	0.094	0.016
PAL	0.196	0.297	–0.063	0.062
ZYG	0.164	0.328	0.002	0.045
RW	0.146	0.361	0.004	0.133
IOW	0.152	0.243	–0.065	0.116
BCW	0.178	0.351	–0.030	0.106
IBW	0.263	0.277	–0.137	–0.025
RH	0.213	0.264	–0.098	0.008
BCH	0.147	0.516	0.030	0.244
BULL	0.169	0.632	0.057	0.312
MZ	0.221	0.151	–0.176	0.092
MU	–0.029	0.147	0.053	0.119
INCW	0.128	0.330	–0.008	0.144
UML	0.262	0.568	–0.214	0.648
M1W	0.095	0.456	–0.055	0.500
M1L	0.278	0.429	–0.243	0.501
M3W	0.093	0.603	–0.038	0.658
M3L	0.104	0.439	–0.064	0.485
LM1L	0.149	0.519	–0.103	0.575
LM1W	–0.005	0.526	0.054	0.558

See Material and Methods for abbreviations.

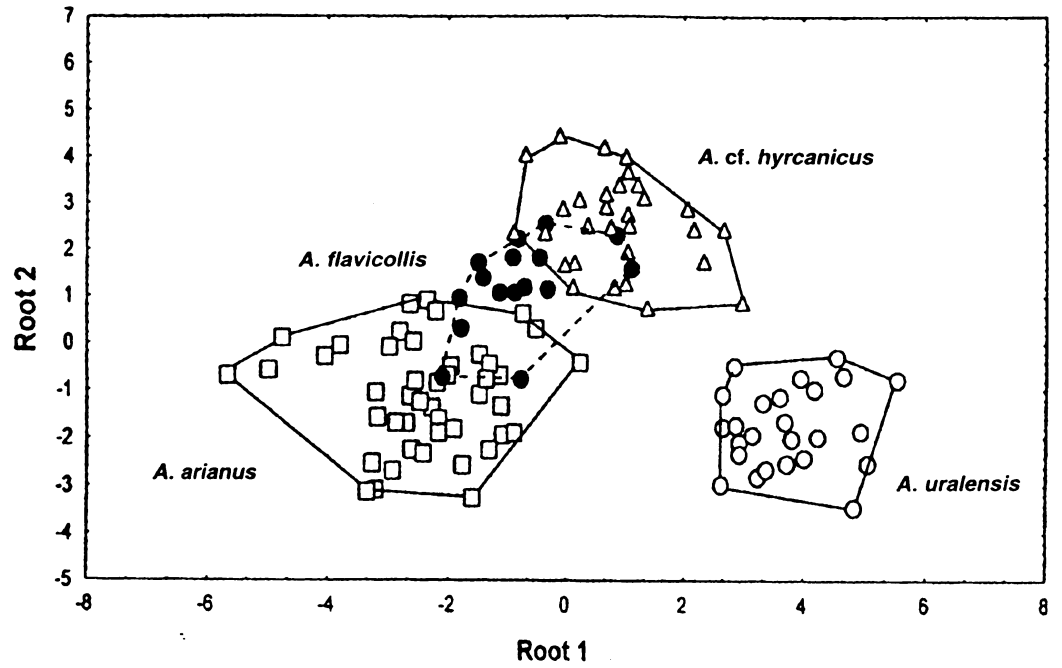

Fig. 4. Projection of samples of four *Apodemus* species onto the first two canonical variates as derived from original nontransformed measurements.

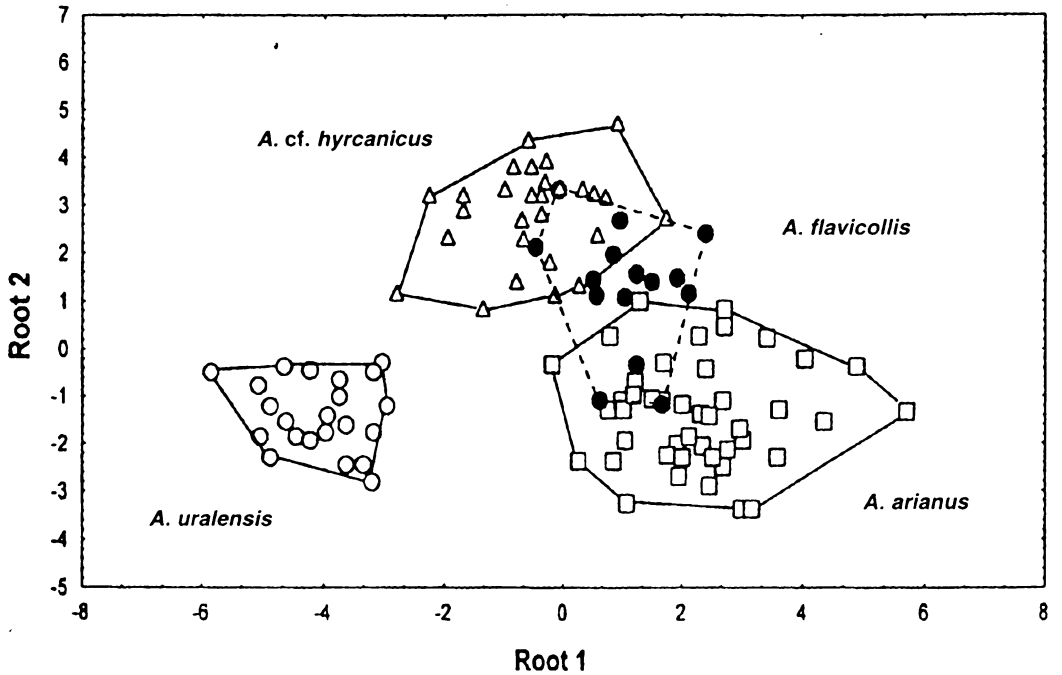

Fig. 5. Projection of samples of four *Apodemus* species onto the first two canonical variates as derived from regression residuals of cranial measurements on the condylobasal length and nontransformed measurements of molars ("size-out" procedure).

or "size-out" data (ccc = 2.375, Wilk's $\lambda = 0.0183$, R = 0.9216, $\chi^2 = 424.01$, $F_{(78, 278)} = 10.05$, $p < 0.0001$) were used. All between-species comparisons were highly significant ($p < 0.0001$). However, slightly better discrimination was obtained from the original measurements (96% of the correctly classified specimens vs. 95% given by the two transformations of the data set). Incorrect classifications (5 or 6 of 122 cases) were recorded, especially between *A. flavicollis* and *A. arianus* (two cases in each direction). One specimen of *A.* cf. *hyrcanicus* was classified as *A. flavicollis*. While the above-mentioned classification errors resulted from all three DFA analyses, another one concerning *A. arianus* classified as *A.* cf. *hyrcanicus* only appeared when using log-transformed or "size-out" data.

To verify the robustness of our classifications, we performed DFAs in which Turkish or Iranian samples of *A. arianus* were excluded from the primary data set and then identified by the resulting discriminant functions: 95.7% and 83.3% of specimens were classified correctly as *A. arianus*, respectively.

The derived simplified classification functions (Table 2) are based on 13 measurements only (ccc = 1.813, Wilk's $\lambda = 0.0337$, R = 0.8756, $\chi^2 = 381.44$, $F_{(39, 314)} = 17.28$, $p < 0.0001$) and classify correctly 116 of 122 specimens (95.1%, in addition to 5 cases classified incorrectly by the complete model, one specimen of *A.* cf. *hyrcanicus* was classified as *A. uralensis*). Variables included into the final model were molar measurements (UML, M1L, LM1L, LM1W), cranial measurements (CBL, FL, IOW, BCH, PAL, MZ, IBW, BULL), and hind foot length (LTP).

Table 2
Discriminant functions derived from the nontransformed measurements by DFA. Thirteen measurements obtained by backward selection were included

	A. uralensis	*A. arianus*	*A. flavicollis*	*A.* cf. *hyrcanicus*
LTP	−4.51	−7.56	−5.99	−5.69
UML	78.72	107.93	95.50	98.79
M1L	128.97	165.57	154.69	131.89
PAL	−16.53	−10.24	−17.30	−11.69
LM1L	7.53	−3.39	29.89	15.13
MZ	20.17	35.99	24.53	29.92
LM1W	247.01	164.83	193.32	240.45
BULL	−38.66	−44.32	−35.10	−31.34
CBL	11.62	20.91	17.10	12.42
FL	14.16	−5.47	2.27	11.22
IOW	165.96	170.07	164.27	178.06
IBW	16.26	24.93	19.89	15.33
BCH	51.28	51.09	57.05	55.40
Constant	−1088.31	−1187.04	−1227.49	−1280.66

See Material and Methods for abbreviations.

DISCUSSION

The divergence of the studied *Sylvaemus* species was a relatively recent event. It was estimated at 850,000 and 1–1.5 million years BP on the basis of the Nei genetic distances (Filippucci et al., 1996; Mezhzherin, 1997b) or 2–4 million years BP computed from DNA sequence divergence (Serizawa et al., 2000). The morphological similarity between the studied species is therefore not surprising. However, the interspecific similarity in our material was very high, as is obvious from the relatively low success of discrimination (96%). It is slightly less than in comparable studies, e.g., that performed on *A. sylvaticus* and *A. flavicollis* in Italy (97%, Panzironi et al., 1994) or that in *A. sylvaticus*, *A. flavicollis,* and *A. alpicola* in the Alps (100%, Reutter et al., 1999). There are only two multivariate studies of *Sylvaemus* species in the regions neighboring our study areas in eastern Turkey, Armenia, and Iran. The first one was done in western Anatolia and two Mediterranean islands by Özkan and Kryštufek (1999) to discriminate *A. flavicollis* from *A. hermonensis* (= *A. arianus*) and *A. sylvaticus*. 96.5% of the specimens were correctly classified. The other study was carried out in the Caucasus (Daghestan) by Lavrenchenko and Likhnova (1995) to discriminate among *A. ponticus*, *A. fulvipectus* (= *A. arianus*), and *A. uralensis* (*A. ponticus* from the Caucasian region is putatively conspecific with the species we refer to as *A. flavicollis*). The percentage of successfully classified individuals is not given, but 95% of the centroids are clearly separated in the scatterplot of canonical axes. The authors reported considerable variation, argued against the use of a single character, and recommended strongly to use multivariate methods for the identification of biochemically undetermined material. Filippucci et al. (1996) described distinct dental characters of each *Sylvaemus* species of western Anatolia and suggested use of a scatterplot of the crown length of the upper molars and bulla length to discriminate between *A. hermonensis* (= *A. arianus*), *A. uralensis,* and *A. flavicollis*. Nevertheless, we found this biplot useless for the discrimination of the material from eastern Turkey, Armenia, and Iran. The same results were obtained when coloration (including the form of pectoral spot) or any other biplot of studied measurements was considered.

We left most of the studied specimens to reach their asymptotic size in captivity. This unusual procedure reduced the age-dependent size variation and allowed us to obtain more realistic estimates of body size than from the samples collected with snap traps in the field. As expected, *A. uralensis* was much smaller than any of the remaining three species. *A. arianus* was the second smallest based on most measurements. However, e.g., body weight of *A. arianus* was about the same as in *A. flavicollis* and *A.* cf. *hyrcanicus,* and according to the mean value, *A. arianus* surprisingly even became the heaviest of the species studied.

Wood mice exhibit postnatal growth of most body and cranial measurements (except for molars) throughout their life span (Frynta and Žižková, 1992). The easiest way to rule out the effect of growth is to perform "size-out" morphometrics. For this purpose it is possible either to consider a single measurement to represent size or to introduce a composite multivariate variable, e.g., Burnaby size (Burnaby, 1966; for application in mice craniometrics, see, e.g., Macholán, 1996). We chose the former approach and

selected the condylobasal length because this measurement well represents the overall skull size and is easily reproducible (see Steiner and Raczynski, 1976). Our finding that the "size-out" procedure produced almost the same results as the analyses based on log-transformed data or nontransformed values ("size-in" procedures) can be attributed to the high age homogeneity of our material. This homogeneity increased the precision of estimations and improved the classification success; however, it limits the applicability of the derived discrimination function to individuals of higher age categories.

A. cf. *hyrcanicus* has been studied morphometrically for the first time. Results of previous biochemical examination of our material (Macholán et al., in press) demonstrated its distinctness, but did not solve the problem of its identity with the material from the type locality of *A. hyrcanicus* in Azerbaijan. Our morphometric results support the view that the Azerbaijanian and Iranian populations belong to a single species. Values of measurements reported by Mezhzherin (1997a) for *A. hyrcanicus* fit well those we found in our sample.

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Appendix 1

Standard descriptive statistics for 27 biometric variables in *A. uralensis*, *A. arianus*, *A. flavicollis*, and *A.* cf. *hyrcanicus* from the Middle East. Statistics given are sample size, mean and standard deviation

Variable	*A. uralensis*			*A. arianus*			*A. flavicollis*			*A.* cf. *hyrcanicus*			Tukey $p < 0.05$
	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	
W	27	21.36	4.12	47	28.50	7.07	16	28.09	7.69	17	27.94	8.25	U < A, F, H
LC	27	92.37	3.48	48	98.00	5.72	16	99.94	6.32	17	101.65	8.61	U < A, F, H
LCD	23	96.09	6.91	43	101.37	7.98	16	103.50	7.81	18	101.00	7.50	U < A, F, H
LTP	27	20.86	0.68	47	21.48	0.89	17	22.64	1.30	23	22.96	0.76	U, A < F, H
LA	26	15.03	0.72	47	16.15	1.02	16	17.26	1.07	20	16.73	1.11	U < A, F, H; A < F
CBL	27	23.21	0.50	48	24.23	0.76	16	25.09	1.02	30	25.03	0.93	U < A < F, H
FL	27	12.18	0.27	48	12.46	0.43	16	12.97	0.44	30	13.12	0.44	U, A < F, H
FI	27	4.91	0.22	48	4.95	0.29	16	5.41	0.30	30	5.14	0.23	U, A < H < F
PAL	27	4.54	0.16	48	4.87	0.26	17	4.85	0.24	30	5.07	0.26	U < A, F < H
ZYG	27	12.86	0.28	47	13.41	0.51	16	13.97	0.65	30	13.90	0.70	U < A < F, H
RW	27	4.58	0.20	47	4.82	0.22	15	4.96	0.24	30	5.11	0.29	U < A, F, H; A < H
IOW	27	4.12	0.12	47	4.31	0.15	16	4.16	0.16	30	4.43	0.16	U, A, F < H
BCW	27	11.19	0.28	48	11.56	0.31	16	11.78	0.34	30	11.88	0.35	U < A, F, H; A < H
IBW	27	8.85	0.21	48	9.39	0.34	16	9.64	0.42	29	9.56	0.36	U < A, F, H
RH	27	4.16	0.16	45	4.45	0.23	16	4.61	0.21	30	4.57	0.27	U < A, F, H
BCH	27	8.82	0.27	47	9.09	0.29	16	9.63	0.43	30	9.62	0.31	U < A < F, H
BULL	27	4.24	0.14	48	4.49	0.23	16	4.97	0.39	30	4.99	0.21	U < A < F, H
MZ	27	0.90	0.11	48	1.11	0.13	17	1.03	0.13	30	1.13	0.17	U < A, F, H
MU	26	0.88	0.11	45	0.87	0.12	16	0.84	0.13	26	0.99	0.16	U, A, F < H
INCW	27	1.34	0.09	48	1.41	0.08	16	1.50	0.10	30	1.50	0.09	U < A < F, H
UML	27	3.59	0.12	48	3.80	0.14	15	3.96	0.13	30	4.02	0.12	U < A < F, H
M1W	26	1.17	0.04	47	1.20	0.05	17	1.27	0.04	29	1.28	0.05	U, A < F, H
M1L	27	1.70	0.07	48	1.82	0.07	17	1.90	0.07	30	1.89	0.07	U < A < F, H
M3W	27	0.79	0.05	47	0.83	0.05	15	0.89	0.06	30	0.96	0.06	U < A < F < H
M3L	27	0.86	0.05	48	0.91	0.07	15	0.93	0.05	30	1.01	0.06	U < A, F < H
LM1W	26	1.03	0.04	48	1.02	0.04	17	1.09	0.05	29	1.12	0.04	U, A < F, H
LM1L	27	1.64	0.07	47	1.70	0.08	17	1.83	0.08	29	1.82	0.06	U < A < F, H

III.

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MULTIVARIATE MORPHOMETRICS OF *APODEMUS MYSTACINUS* IN THE NEAR EAST AND ITS DIVERGENCE FROM EUROPEAN *A. M. EPIMELAS* (MAMMALIA: RODENTIA)

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ABSTRACT

Morphometric variation in *Apodemus mystacinus* populations from Syria and Jordan was studied and compared with those in Turkey, Greece, Bulgaria, and the former Yugoslavia. Altogether, 270 specimens of *A. mystacinus* were examined by multivariate procedures based on molar, skull, and body measurements. The previously reported distinctness of the European subspecies (species) *epimelas* and Asian *mystacinus* was confirmed. Asian populations are fairly homogenous. The populations from Syria and Jordan, as well as other material examined from Turkey, corresponded well with the population of the Middle Taurus Mts., Turkey (*terra typica* of *A. m. mystacinus*). The only exception was the case of a slightly different population from the Al-Duruz Mts. (S Syria). The validity of sspp. *euxinus* (E Pontic Mts.) and *pohlei* (N. Syria) was not supported by our data.

INTRODUCTION

The rock mouse, *Apodemus mystacinus* (Danford et Alston, 1877), is a specialized petricolic Eastern Mediterranean rodent species. It is confined to rocky and stony surfaces (bare rocks, stone walls, ruins, etc.) in various environments, e.g., macquis, woodlands, and cultivated areas with a lot of clefts and at least some scattered vegetation. Its range extends from the Balkan Peninsula, i.e., the former Yugoslavia, Albania, Bulgaria, and Greece (for a recent review, see Mitchell-Jones et al., 1999) to the Near East: Turkey, Transcaucasia, Syria, Jordan, Lebanon, Israel, and Iraq (Kock et al., 1972; Harrison and Bates, 1991). It has been also recorded on some islands in the Eastern Mediterranean (Storch, 1977; Niethammer, 1978).

Traditionally, two subspecies have been recognized: *A. m. mystacinus* (Danford et Alston, 1877)—*terra typica*: Zebil, the Bolkar Dağlari Mts., Asia Minor; and *A. m. epimelas* (Nehring, 1902)—*terra typica*: Agoriani, the Parnas Mts., Greece. The

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nominotypic subspecies extends throughout the Asian part of the range, the western Aegean Islands, and Crete (Storch, 1977), while *epimelas* is distributed in Europe and may be recognized by its larger size (longer hind foot, larger condylobasal length, etc.) and dental characters (Mirić, 1966; Spitzenberger, 1973; Storch, 1977). In his systematic revision of the *Apodemus* species of Northern Eurasia, Mezhzherin (1997) listed *A. epimelas* as an independent species. Recently, allozyme analysis by Filippucci et al. (2002) has also supported this view because they found that the genetic differentiation between European and Asian populations corresponded to that generally observed between morphologically well-differentiated small mammal species. This opinion coincides with the results of an earlier morphological study by Storch (1977), who suggested that these subspecies may be elevated to species level.

There are several studies dealing with the morphometrics of *A. mystacinus*, and extensive data are available from the territory of the former Yugoslavia (Mirić, 1964; 1966), Bulgaria (Pechev, 1962), Greece (Ondrias, 1966), Crete (Zimmermann et al., 1953), and Georgia (Šidlovskij, 1953). Moreover, populations in Asia Minor and neighboring areas were thoroughly studied by univariate morphometric methods (Spitzenberger, 1973). On the basis of the original data and an extensive review of literature data, Spitzenberger (l. c.) reported a clinal decrease in the length of the upper molar row from the Balkans along the Mediterranean coast of Anatolia as far as Israel (but measurements from the Pontic area were similar to those from the southernmost part of the range). A similar west–east cline along the southern Anatolian coast was also found in the upper molar width. In spite of geographic variation, Spitzenberger (1973) considers Anatolian populations to belong to a single subspecies. Nevertheless, there are additional subspecific names available: *smyrnensis* Thomas, 1903—*terra typica*: Smyrna (= İzmir), western Asia Minor; *euxinus* Allen, 1915—*terra typica*: Scalita (= Altindere), Trabzon, Eastern Pontic Mts.; *pohlei* Aharoni, 1932—*terra typica*: Kafrun, Nussarijeh Mts., Northern Syria; and *rhodius* Festa, 1914—*terra typica*: Aghios Isidoros, Rhodes Island, Greece. The validity of these taxa has already been questioned by Ellermann (1948), Mirić (1966), and Spitzenberger (1973), and their systematic revision is needed.

Although the presence of *A. mystacinus* was repeatedly reported from Syria, Lebanon, Israel, and Jordan (e.g., von Lehmann, 1965; Lewis et al., 1967; Atallah, 1977; Harrison and Bates, 1991; Benda and Sádlová, 1999; Shehab et al., 1999), morphometric data from this region are still scarce. The only exception is a detailed study by Tchernov (1979) concerned with the development of M^1 length in Israeli populations, in the period from the Middle Pleistocene till the present.

The aims of this study were to: (1) evaluate morphometric variation within and among four populations of *A. mystacinus* from Syria and Jordan, (2) to compare them with samples coming from other geographic regions, including those from the *terra typica* population of *A. mystacinus* from the Middle Taurus Mts., and (3) to compare multivariate morphometric distances within and between subspecies/species *mystacinus* and *epimelas* coming from different parts of the distributional range of *Apodemus mystacinus* (the Balkans, Turkey, Syria, Jordan). In spite of previous attempts (e.g., Zimmermann 1953, Mirić 1964, Spitzenberger 1973), multivariate statistical methods dealing with "size out" data are introduced for the first time to analyze interpopulation variation of this species.

MATERIAL AND METHODS

The material was collected by the authors and their colleagues during field trips to the former Yugoslavia (1974–1978), Bulgaria (1981—1984), Greece (1985–1995), Turkey (1993–2000), Syria (1998–2001), and Jordan (1995); it is deposited in the collections of the Department of Zoology, Charles University, Prague (Nos. BB 266–2721; BJ 266–3822; BG 3733–4582; TU 161–1171; MISC 141–333; SUR 1–37) and in the zoological collections of the National Museum, Prague (Nos. P6V 48220–49634). In total we studied 270 specimens from the following 30 localities, depicted in Fig. 1.

FORMER YUGOSLAVIA

(1) Makarska, 43° 18′ N, 17° 01′ E, Croatia, ca. 300 m asl, N = 2; (2) Stara Podgora, Podgora, 43° 16′ N, 17° 08′ E, Croatia, ca. 600 m asl, N = 1; (3) Kotezi, Popovo polje, 42° 55′ N, 18° 00′ E, Bosnia-Hercegovina, 350 m asl, N = 1; (4) Virpazar, 42° 15′ N, 19° 06′ E, Montenegro, 30 m asl, N = 1; (5) 2 km S of the town Peštani, 40° 59′ N, 20° 49′ E, distr. Ohrid, Macedonia, ca. 700 m asl, N = 1.

BULGARIA

(6) Gorna Breznica, 41° 47′ N, 23° 09′ E, distr. Blagoevgrad, 400 m asl, N = 90.

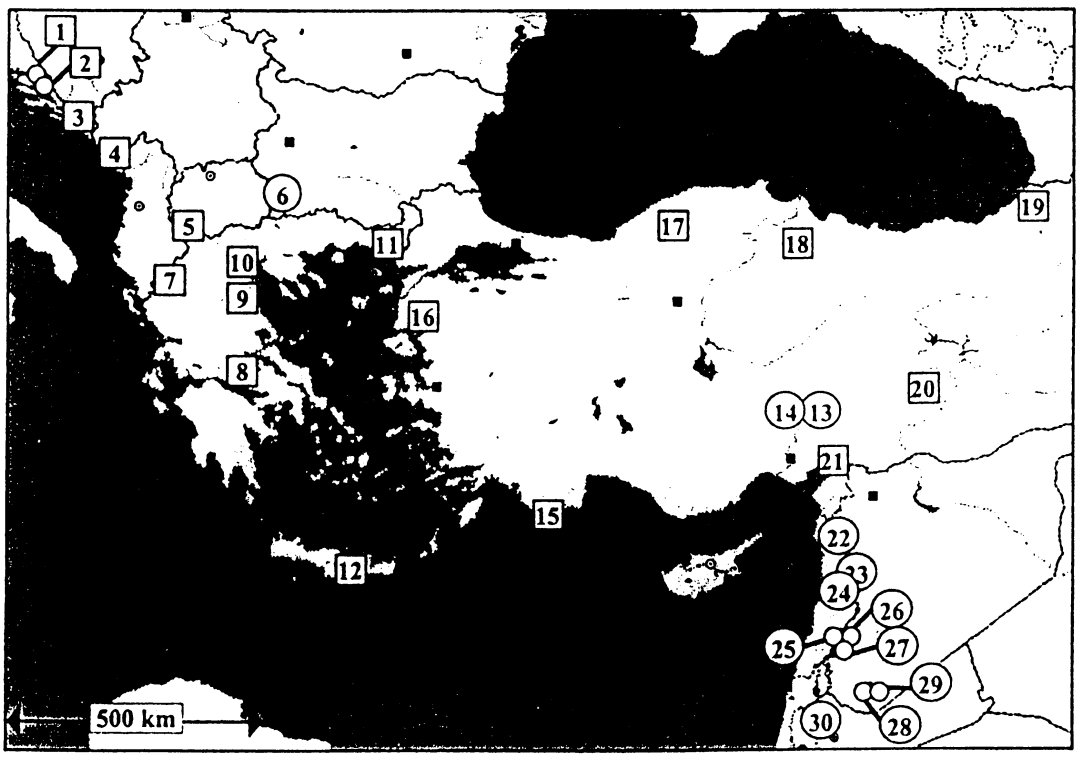

Fig. 1. Survey of the sample localities. For locality numbers see text (circles—main study populations used in DFA).

GREECE

(7) Papiggo, 39° 58′ N, 20° 43′ E, distr. Ioannina, 1000 m asl, N = 7; (8) Delphi, 38° 29′ N, 22° 31′ E, distr. Fokida, ca. 600 m asl, N = 2; (9) Ano Skotina, 40° 01′ N, 22° 32′ E, distr. Pieria, 700 m asl, N = 1; (10) Monastery Timiou Prodromou, 40° 28′ N, 22° 15′ E, distr. Veria, 200 m asl, N = 3; (11) Mt. Kerveros , 41° 09′, N, 25° 53′, E, distr. Alexandroupoli, ca. 800 m asl, N = 1.

CRETE

(12) Psychro, 35° 11′ N, 25° 27′ E, distr. Lasithí, ca. 1300 m asl, N = 2.

TURKEY

The Taurus Mts.: (13) Feke, 37° 49′ N, 35° 55′ E, distr. Adana, ca 600 m asl, N = 11; (14) Yazlik, 37° 44′, N, 35° 23′, E, distr. Adana, ca. 1200 m asl, N = 6.

OTHER TURKEY: (15) Kaş, 36° 12′ N, 29° 36′ E, distr. Antalya, ca. 30 m asl, N = 3; (16) 10 km SE from Çirpilar, 39° 45′ N, 26° 57′ E, distr. Çanakkale, ca. 1000 m asl, N = 2; (17) 5 km N from Safranbolu, 41° 17′ N, 32° 41′ E, distr. Zonguldak, 500 m asl, N = 3; (18) Seyfe; 40° 50′ N, 35° 55′ E, distr. Amasya, N = 5; (19) Damar, 41° 15′ N, 41° 34′ E, distr. Artvin, 1000 m asl, N = 5; (20) Mt. Nemrud Dağ, 38° 01′ N, 38° 30′ E, distr. Adiyaman, ca. 1000 m asl, N = 1; (21) Yukari Karafakili, 36° 47′ N, 36° 27′ E, distr. Hatay, ca. 600 m asl, N = 2.

Note: localities 17 and 18 are referred to as E Pontic Mts. and localities 19 and 20 as SE Turkey.

SYRIA

The An-Nusairiah Mts.: (22) 5 km S from Slinfeh, 35° 36′ N, 36° 12′ E, distr. Latakiah, 1350–1450 m asl, N = 19; (23) 5 km W from Ash'meiseh, 34° 56′ N, 36° 50′ E, distr. Hama, 850 m asl, N = 7; (24) 5 km S from Safita, 34° 49′ N, 36° 10′ E, distr. Tartus, 210 m asl, N = 1.

The Hermon Mts.: (25) Bloudan, 33° 44′ N, 36° 08′ E, distr. Damascus, 1560 m asl, N = 10; (26) Sarghaya, 33° 50′ N, 36° 10′ E, distr. Damascus, ca. 1330 m asl, N = 1; (27) Barqash, 33° 29′ N, 36° 00′ E, distr. Damascus, 1370 m asl, N = 4.

The Al-Duruz Mts.: (28) Quanawat, 32° 44′, N, 36° 37′, E, distr. Suwayda, N = 61; (29) Sia, 32° 43′, N, 36° 39′, E, distr. Suwayda, ca. 1470 m asl, N = 1.

JORDAN

The Ajlun Mts.: (30) Mt. Ajlun, 32° 21′, N, 35° 44′, E, dist. Irbid, ca. 1000 m asl, N = 16.

During evaluations we pooled some localities because of their geographic proximity. They are further referred to by country or geographic region (e.g., Taurus Mts., E Pontic Mts., W Turkey, SE Turkey, other Turkey, etc.). In the majority of specimens all measurements were evaluated, the only exception being 56 specimens (G. Breznica, N = 54; Podgora, N = 1; Papiggo, N = 1) consisting mostly of juveniles or specimens with damaged skulls; here only molar measurements were used.

Standard external measurements were taken with callipers accurate to the nearest mm (body length—LC, tail length—LCD) or 0.1 mm (ear length—LA, hind foot length—

LTP). The skulls were biologically prepared using *Dermestes* larvae. The following 14 cranial measurements were taken with the use of callipers accurate to the nearest 0.1 mm (13 characters) or under a stereomicroscope accurate to the nearest 0.05 mm (FI): CBL—condylobasal length, FL—facial length, PAL—palatal length, ZYGW—zygomatic breadth, RW—rostral width (maximum distance), IOW—interorbital width (minimum distance), BCW—brain-case width, IBW—interbullar width (shortest distance between left and right porus acusticus externus), RH—rostral height, BCH—brain-case height, BULL—bulla length, FI—length of foramen incisivum, and MZ, MU—width of choanae (see Fig. 2). Eight tooth measurements (molars measured on the crowns as maximal distances) were taken with the use of a stereomicroscope: UML—upper molar row length (to the nearest 0.05 mm), M1L—first upper molar length, M1W—first upper molar width, M3L—third upper molar length, M3W—third upper molar width, LM1L—first lower molar length, LM1W—first lower molar width, INCW—upper incisor width (measured from the side view, below os incisivum, *fide* Steiner 1968) (to the nearest 0.014 mm). Molar abrasion according to Steiner (1968) was assessed using a stereomicroscope.

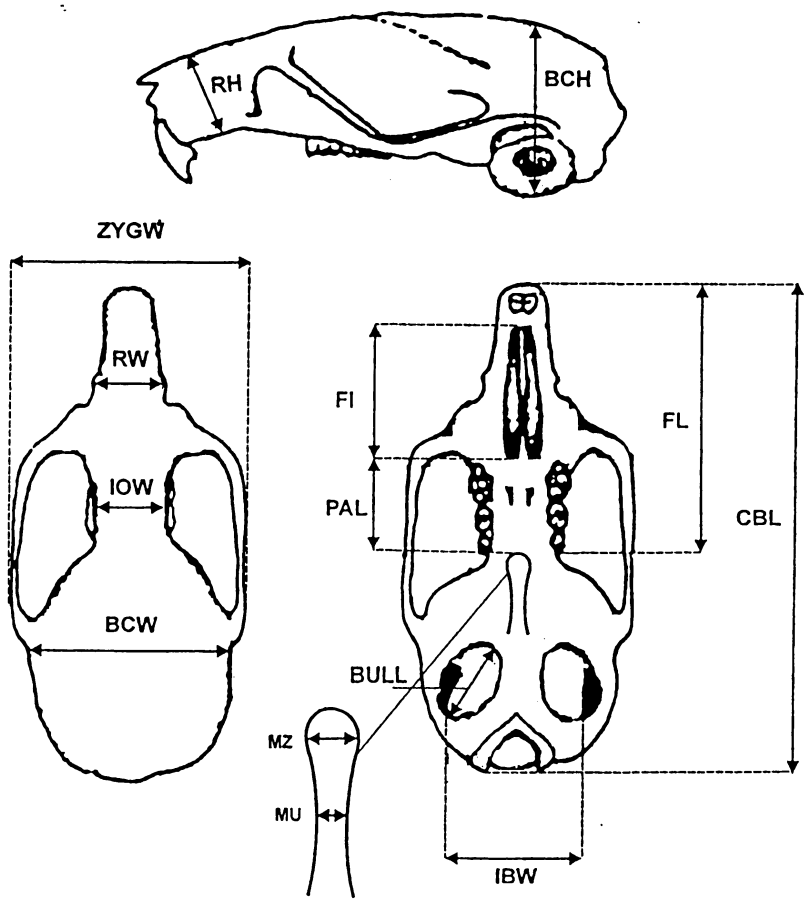

Fig. 2. Skull measurements (teeth measurements are not depicted). See text for explanation of the measurement abbreviations.

First, the data were log-transformed prior to further procedures. (1) Molar measurements exhibiting no postnatal growth (Spitzenberger, 1973; Frynta and Žižková, 1992) were further treated by Principal Component Analysis (PCA) to obtain a single composite variable reflecting molar size. PC 1 scores were further treated by ANOVA in order to evaluate the variation amongst the study populations; Tukey tests for unequal n were applied. (2) We computed residuals from the regression of each measurement (except those concerning molars) on facial length. To avoid possible differences in allometries between European *A. m. epimelas* and Asian *A. m. mystacinus* sensu lato, the regression lines were estimated on the basis of the Asian material only. The intercept and slope coefficients of regression lines for each measurement were: LC (0.5278; 1.5705), LCD (1.4957; 1.2437), LTP (2.3338; 0.3234), LA (1.7147; 0.4650), FI (–0.8260; 1.0132), PAL (–0.2994; 0.7695), MZ (1.510; –0.2684), MU (1.7042; –0.4918), BULL (0.3730; 0.4427), INCW (–3.9884; 1.6550), CBL (0.2762; 1.1382), RW (–0.7328; 0.8747), ORBW (0.7664; 0.2888), BCW (1.7099; 0.3325), IBW (0.8013; 0.5757), RH (–2.2303; 1.4291), BCH (1.0016; 0.5163), ZYGW (0.1069; 0.9736), respectively. Residuals were used to rule out the effect of growth and size. This data set, consisting of molar measurements and residuals of the other measurements, was further subjected to Discriminant Function Analysis (DFA). Codes of six well-represented populations, i.e., G. Breznica, the Middle Taurus Mts. (Feke, Yazlik,), the An-Nusairiah Mts. (Slinfeh, Ash' meiseh, Safita), the Hermon Mts. (Bloudan, Burqush, Sarghaya), the Al-Duruz Mts. (Quanawat, Sia), and the Ajlun Mts. were used as the grouping variable. Values of DFA roots were computed and plotted, as were those for mice from other localities (not included in the primary analysis). To evaluate morphometric differences between populations we computed Mahalanobis distances using Canonical Vector Analysis (CVA) based on pooled variance–covariance matrices (NTSYS version 1.80). UPGMA clustering was used to construct phenetic trees. The significance of the morphometric distances was assessed by Hotelling tests: $F = (n_1 + n_2 - p - 1) / ((n_1 + n_2 - 2) \times p) \times T^2$; $T^2 = D^2 \times (n_1 \times n_2) / (n_1 + n_2)$; $df_1 = n_1 + n_2 - p - 1$; $df_2 = p$; p = number of variables in matrix; n_1 and n_2 = sample sizes; D = Mahalanobis distance between samples.

The data were checked for normality prior to the statistical analyses, deviations from normality were small, and most distributions were both unimodal and symmetrical as required for the multivariate procedures used. The STATISTICA Analysis System (release 6.0) was used for most calculations.

RESULTS

To assess the main patterns of morphometric divergence on a large scale, we pooled specimens from localities of the same geographic region into broader samples and computed generalized distances. As obvious from the UPGMA tree (Fig. 3), the European and Asian branches were well-separated. The Mahalanobis distances (D) between European and Asian samples varied within the range 6.21–7.66; those concerning large samples were significant when treated by the Hotelling test: e.g., G. Breznica vs. the Al-Duruz Mts. (D = 6.65, F = 4.54, $p < 0.01$), G. Breznica vs. the An-Nusairiah Mts.

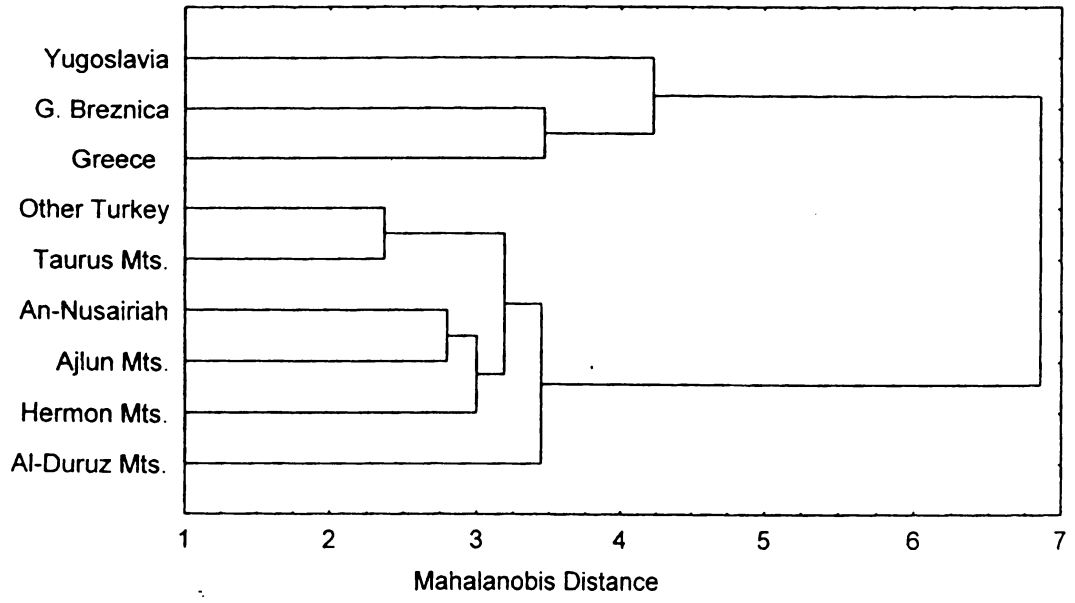

Fig. 3. UPGMA phenetic tree based on Mahalanobis distances.

(D = 7.08, F = 2.65, $p < 0.01$), and Greece vs. the Al-Duruz Mts. (D = 6.53, F = 1.88, $p < 0.05$). The distances amongst samples within Europe and Asia were much smaller (D = 3.46–4.43 and D = 2.37–3.97, respectively) and none were significant.

Next, six well-represented populations (see Material and Methods) were treated by DFA (Wilk's $\lambda = 0.016$, R = 0.937, $\chi^2 = 649.5$, $F_{(125, 708)} = 7.506$, $p << 0.001$). The classification success was 100% in the sample from G. Breznica (the only European population included) and 63–81% in five Asian populations. Then the resulting classification function was applied to overall material also including the animals from other populations (less represented). No classification/reclassification mistakes between *A. m. epimelas* and *A. m. mystacinus* were found. All the specimens from continental Europe were assigned to the G. Breznica sample, and the specimens from Asia (as well as those from Crete) to any of the five Asian populations. Relationships between the study populations in morphospace were visualized by a plot of canonical roots (Fig. 4, see Table 1 for loadings). The overall variation within *A. m. epimelas* is somewhat broader than can be inferred solely from the largest sample from Bulgarian G. Breznica. However, there is a substantial overlap between samples from Greece and those from both the former Yugoslavia and Bulgaria. The position of specimens from Delphi (the Parnas Mts.) close to type locality of *epimelas* (Agoriani, the Parnas Mts.) is not exceptional. Concerning Asian populations, the most distinct is the position of the population from the Al-Duruz Mts. in soutwest Syria, which is somewhat displaced along the root 2 axis. The convex polygons of the other populations studied, including that from the Middle Taurus Mts. (where type locality of *A. mystacinus* is situated) overlap considerably.

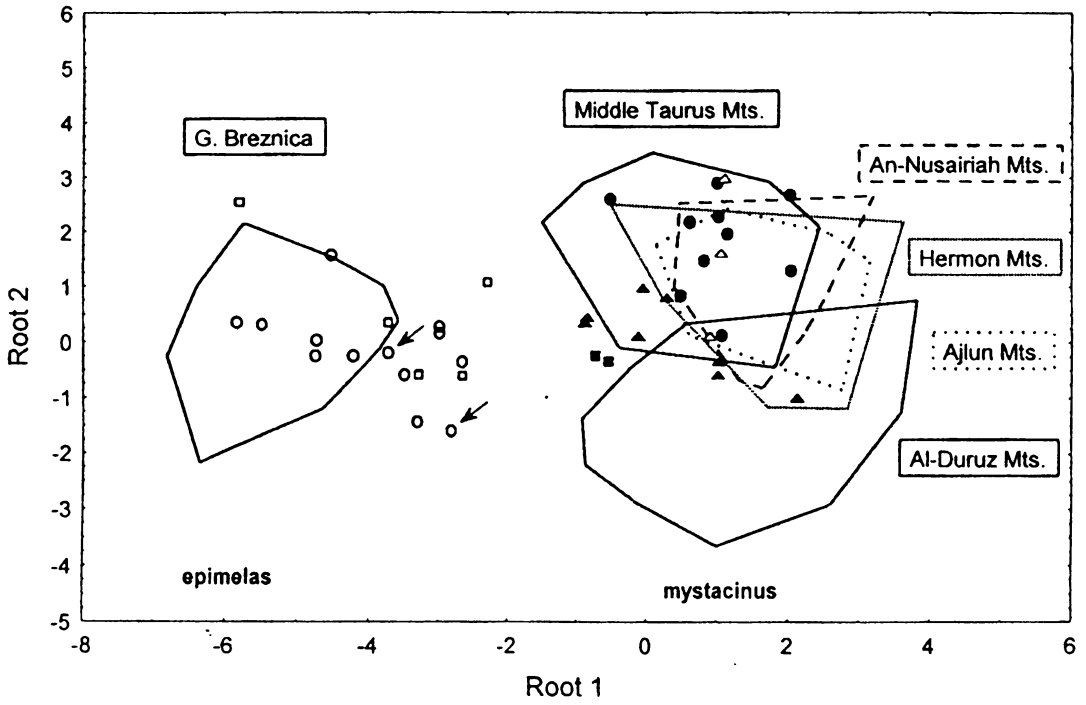

Fig. 4. Projection of samples of *Apodemus mystacinus* study populations onto the first two canonical roots as derived from Discriminant Function Analysis (DFA) based on residuals (regression on the facial length) and original molar measurements. Polygons represent main populations used in DFA. Open circles— Greece (Delphi with arrows), open square—former Yugoslavia, solid circles—Pontic Mts., open triangle—SE Turkey, solid triangle—W Turkey, solid square—Crete.

PC 1 scores computed from molar measurements may be interpreted as molar size (for loadings, see Table 2). ANOVA results confirmed the variation among populations ($F_{13, 256} = 44.97$, $p < 0.0001$): the highest values were found in European populations (slightly increasing southwards from former Yugoslavia to Greece), intermediate ones on the island of Crete, western Turkey, the Middle Taurus Mts., and the Al-Duruz Mts., while the lowest values were found in northeastern and southeastern Turkey, and the rest of Syria and Jordan (Fig. 5). Accordingly, Tukey comparisons (for unequal N) revealed significant differences ($p < 0.05$) between well-represented European and Asian samples. These differences are not surprising; they just support the demonstrated divergence of European and Asian populations. More interesting are the significant comparisons within Asia. Molars of populations from the Middle Taurus Mts. and the Al-Duruz Mts. are bigger than those in other populations from Syria (Al-Nusairiah Mts., Hermon Mts.) and Jordan. The population means of molar measurements are given in Table 3, those of other measurements (only specimens of molar abrasion category four and higher) are shown in Table 4.

Table 1

Canonical variate loadings for 25 body, cranial and teeth measurements. DFA analysis based on residuals from regression on facial length (in measurements exhibiting postnatal growth) and original measurements of molars. See text for explanation of measurement abbreviations

	UML	M1W	M1L	M3W	M3L	LM1L	LM1W	LC	LCD	LTP	LA	FI	PAL
Root 1	–0.384	–0.461	–0.255	–0.182	0.186	–0.337	–0.413	–0.052	0.019	–0.110	–0.118	–0.109	0.085
Root 2	–0.325	–0.107	–0.377	–0.053	0.042	–0.271	–0.126	0.404	0.186	0.392	–0.147	–0.013	–0.023

	MZ	MU	BULL	INCW	CBL	RW	IOW	BCW	IBW	RH	BCH	ZYGW
Root 1	–0.227	0.146	–0.079	0.054	0.248	–0.128	0.046	0.004	–0.013	0.221	–0.073	0.305
Root 2	–0.072	–0.039	–0.252	0.101	–0.183	0.251	0.046	–0.081	–0.352	0.116	–0.147	–0.106

Table 2

PC 1 loadings for 7 molar measurements. See text for explanation of measurement abbreviations

	UML	M1W	M1L	M3W	M3L	LM1L	LM1W	Expl.Var	Prp.Totl
PC 1	0.95	0.90	0.89	0.31	0.59	0.88	0.92	4.57	0.65

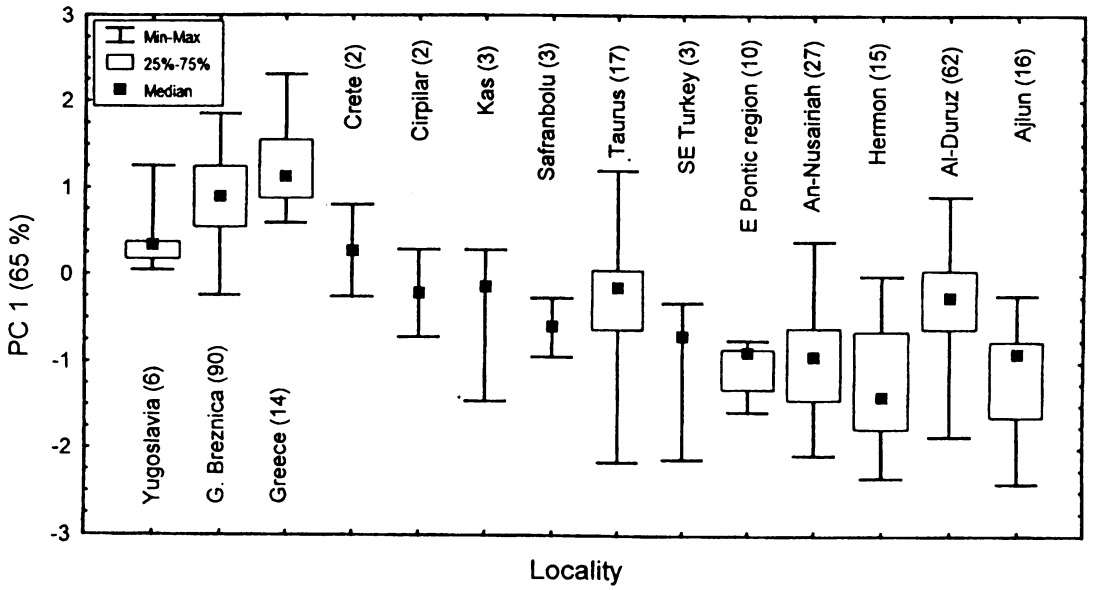

Fig. 5 Box plots of PC 1 scores derived from molar measurements. Sample sizes are given in parentheses.

Table 3

Standard descriptive statistics for seven teeth measurements in study samples of *Apodemus mystacinus*. Statistics given are sample size (N), mean (in mm), and standard deviation (S.D.). See text for explanation of measurement abbreviations

	Yugoslavia			G. Breznica			Greece			Taurus Mts.			Other Turkey		
	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.
UML	4.84	6	0.09	4.96	90	0.10	5.00	14	0.11	4.64	17	0.13	4.54	21	0.10
M1W	1.52	6	0.04	1.54	90	0.04	1.56	14	0.04	1.46	17	0.05	1.42	21	0.05
M1L	2.33	6	0.05	2.42	90	0.07	2.48	14	0.08	2.27	17	0.08	2.22	21	0.07
M3W	1.06	6	0.05	1.04	90	0.05	1.07	14	0.04	1.10	17	0.06	1.06	21	0.04
M3L	1.12	6	0.04	1.12	90	0.05	1.13	14	0.06	1.12	17	0.05	1.09	21	0.05
LM1L	2.25	6	0.02	2.29	90	0.06	2.33	14	0.07	2.16	17	0.07	2.16	21	0.08
LM1W	1.33	6	0.02	1.37	90	0.03	1.39	14	0.05	1.29	17	0.05	1.25	20	0.05

	An-Nusairah Mts.			Hermon Mts.			Al-Duruz Mts.			Jordan		
	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.
UML	4.54	27	0.10	4.50	15	0.13	4.70	62	0.16	4.57	16	0.14
M1W	1.41	27	0.04	1.37	15	0.05	1.43	62	0.04	1.38	16	0.05
M1L	2.23	27	0.08	2.23	15	0.06	2.33	62	0.09	2.26	16	0.07
M3W	1.04	27	0.05	1.01	15	0.06	1.05	61	0.04	1.03	16	0.05
M3L	1.07	27	0.05	1.04	15	0.07	1.09	62	0.06	1.03	16	0.06
LM1L	2.13	27	0.07	2.14	15	0.07	2.19	62	0.05	2.14	16	0.07
LM1W	1.25	27	0.05	1.23	15	0.04	1.27	62	0.04	1.22	16	0.05

Table 4

Standard descriptive statistics for 19 skull and external measurements in 5 study samples of *Apodemus mystacinus* (only adult animals with abrasion category of 4–6 are considered). Statistics given are sample size (N), mean (in mm), and standard deviation (S.D.). See text for explanation of measurement abbreviations

	G. Breznica			Taurus Mts.			Other Turkey			Syria & Jordan			Al-Duruz Mts.		
	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.	Mean	N	S.D.
LC	121.6	25	4.66	113.4	12	7.40	112.0	9	6.20	117.7	23	5.17	113.7	17	7.51
LCD	128.9	18	5.18	123.6	10	8.47	118.1	7	2.61	127.6	20	8.42	124.4	13	10.97
LTP	25.3	24	0.89	24.4	12	0.93	24.5	9	0.64	25.0	23	0.89	24.3	17	1.01
LA	20.5	22	0.95	19.3	12	0.65	18.6	9	1.32	19.3	21	1.01	19.6	17	1.38
FI	6.97	26	0.25	6.53	12	0.33	6.36	10	0.36	6.58	24	0.29	6.58	17	0.22
PAL	5.87	26	0.24	5.63	12	0.25	5.68	9	0.37	5.81	23	0.25	5.83	17	0.25
MZ	1.72	26	0.11	1.56	12	0.08	1.54	10	0.10	1.52	23	0.10	1.54	16	0.16
MU	1.33	22	0.11	1.50	11	0.12	1.47	6	0.15	1.49	24	0.13	1.50	15	0.19
BULL	4.89	25	0.12	4.71	12	0.10	4.55	8	0.19	4.67	24	0.17	4.79	17	0.16
INCW	1.61	26	0.06	1.56	12	0.06	1.49	10	0.08	1.59	24	0.06	1.56	17	0.10
CBL	28.10	24	0.53	26.85	11	0.85	26.21	7	0.65	27.64	22	0.67	27.97	14	0.94
FL	15.05	26	0.25	14.30	12	0.40	14.13	10	0.46	14.54	24	0.32	14.58	17	0.39
RW	5.28	26	0.18	5.03	12	0.24	4.94	10	0.21	5.07	24	0.21	4.98	17	0.17
IOW	4.70	26	0.14	4.71	12	0.17	4.54	10	0.18	4.65	24	0.17	4.60	17	0.19
BCW	13.62	22	0.28	13.27	9	0.28	13.15	8	0.35	13.48	21	0.31	13.56	14	0.40
IBW	10.63	25	0.19	10.07	10	0.18	10.02	6	0.22	10.35	22	0.32	10.48	12	0.31
RH	4.98	26	0.14	4.80	12	0.18	4.72	10	0.20	4.98	24	0.19	4.99	17	0.25
BCH	11.18	24	0.23	10.61	10	0.40	10.59	8	0.29	10.77	23	0.20	10.86	14	0.38
ZYGW	14.90	25	0.31	14.56	12	0.34	14.26	9	0.49	15.20	24	0.47	15.35	16	0.49

DISCUSSION

As expected, our results strongly support the distinctness of the taxa *mystacinus* and *epimelas*. Their degree of morphometric differentiation is high, corresponding well with the recent findings of allozyme analysis (Filippucci et al., 2002) that reopened the question of the possible elevation of *epimelas* to species level. On the other hand, the geographic variation within both *mystacinus* and *epimelas* was rather low. Further subspecific splitting of *A. mystacinus* was not supported by our morphometric data. Most specimens from populations near the type locality of *pohlei* (Al-Nusairiah Mts., Syria) and *euxinus* (E Pontic Mts., NE Turkey) are situated in the morphospace just within the convex polygon of *A. mystacinus* from the topotypic region (Middle Taurus Mts.). Also the specimens from Crete (sometimes assigned to subspecies *rhodius*, see Zimmermann et al., 1953) accord well with the morphometric pattern of Asian populations; this is in accordance with the opinion of previous authors (e.g., Storch, 1977). The population from the Al-Duruz Mts. seems to be the most differentiated from other Asian populations studied, and it can be attributed to the geographic isolation of *A. mystacinus* populations in this locality. The Al-Duruz Mts. is the easternmost forested area in southern Syria supporting a permanent population of this species, all other mountain regions in the Mediterranean part of the country being separated from the Al-Duruz Mts. by desert. Morphometric variation between *epimelas* samples seems to be comparable to that between *mystacinus* ones. The morphospace position of specimens from the vicinity of the *epimelas* type locality in the Parnas Mts. conforms to the pattern of variation in the entire European sample. The evaluation of *epimelas* variation is, however, premature and further research based on larger samples is needed.

Some authors reported a west–east clinal decrease of molar size in Asia Minor (von Lehmann, 1965; Spitzenberger, 1973). Our data (Table 3) revealed gradual decrease in M1W, M3L, M3W, and LM1W from the Middle Taurus Mts. southwards into Jordan. Only the exceptional Al-Duruz Mts. population (discussed above) does not follow this trend and possesses considerably larger molars. Syrian mice with conspicuously narrow molars were reported by Ellermann (1948) and von Lehmann (1965). Small molars in Syrian and Jordanian mice can perhaps be explained by character release in the absence or scarcity of smaller *Apodemus* species, similar to the phenomenon described by Tchernov (1979) in Israeli populations. It should be mentioned that, with the exception of Slinfeh, Syria and Ajlun Mt., Jordan (where also *A. flavicollis* resp. *A. hermonensis* were collected), in all our other Levantine localities *A. mystacinus* was the only species of the genus.

Clinal variation was not obvious when general molar size expressed as PC 1 of molar measurements was considered (Fig 5). However, populations from the Al-Duruz Mts. (Syria), the Taurus Mts. (Turkey), western Turkey, and Crete were found to have bigger molars than the other populations studied. When the case of the Al-Duruz Mts. is omitted, this may confirm the differences between western and eastern populations reported by Spitzenberger (1973).

Although the values of UML in our Balkan sample (Table 3) are somewhat lower than those reported by Mirić (1964, 1966), Kahmann (1964), and Ondrias (1966), they

do correspond with the general opinion that Yugoslavian and Bulgarian *A. mystacinus* are smaller than Greek ones (Niethammer, 1978). The same trend is also obvious in Fig. 5.

The multivariate morphometric approach confirmed considerable differences between Asian and European *A. mystacinus* populations. As a next stage in the study, it would be most desirable to check also the status of populations inhabiting the Aegean Islands. According to Storch (1977), their molar morphology suggests they mostly belong to Asian stocks.

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IV.

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Skull shape in the genus *Apodemus*: phylogenetic conservatism and/or adaptation to local conditions

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Frynta D., Mikulová P. and Vohralík V. 2006. Skull shape in the genus *Apodemus*: phylogenetic conservatism and/or adaptation to local conditions. Acta Theriologica 51: 139–153.

We studied morphological variation among western Palaearctic species of woodmice (genus *Apodemus*). Twenty one dental and skull variables were measured and evaluated using multivariate statistical approaches. A total of 501 specimens of the following 9 species of wood mice were examined: *A. hermonensis*, *A. hyrcanicus*, *A. uralensis* (= *microps*), *A. flavicollis*, *A. sylvaticus*, *A. epimelas*, *A. mystacinus*, *A. peninsulae*, *A. agrarius*. Species occupying large geographic areas were represented by two or three geographically distant populations. The analyses, based both on original and size adjusted data, revealed congruence between morphological evolution and phylogenetic relationships.

The integrity of major clades was supported by morphometric trees. Conspecific samples showed a clear tendency to cluster together regardless of ecological differences and geographical distances. This finding may suggest that studied traits exhibit evolutionary conservatism, and therefore are not fully determined by actual selective pressures. Besides this, we demonstrated that morphological differentiation of taxa belonging to the subgenus *Sylvaemus* was more pronounced in Central Europe than in the Near East. This observed phenomenon could be of adaptive nature.

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Key words: morphometrics, wood mice, *Sylvaemus*, *Karstomys*

Introduction

Wood mice of the genus *Apodemus* Kaup, 1829 are common murid rodents in the Palaearctic region (cf Musser *et al.* 1996, Mitchell-Jones *et al.* 1999). Their initial radiation most likely started somewhere in Central or Eastern Asia (Musser *et al.* 1996, Serizawa *et al.* 2000, Suzuki *et al.* 2003) and resulted in divergence into two or three Asian clades and a single European clade. Most species of the genus *Apodemus* found in Europe, North Africa and Western Asia belong to the European clade which comprises the subgenera *Karstomys* Martino, 1939 (including two petricolous species: *A. mystacinus* (Danford et Alston, 1877) and *A. epimelas* (Nehring, 1902)) and *Sylvaemus* Ognev, 1924 (including at least six species as discussed below, Musser *et al.* 1996, for genetic support see eg Martin *et al.*

2000, Michaux *et al.* 2002, Bellinvia 2004). The only Western Palaearctic representative of the East Asian clade (subgenus *Apodemus*) is *A. agrarius* (Pallas, 1771), a field-dwelling species that extended its range from Eastern Asia westwards to Europe relatively recently in the Holocene (Böhme 1978). In the western Palaearctics, field identification of the three subgenera is easy (*A. agrarius* – black vertebral stripe, *Karstomys* – large size and grey pelage, *Sylvaemus* – uniform brown pelage on the back), but species identification of specimens of the subgenus *Sylvaemus* has been a perpetual problem for both field zoologists and rodent taxonomists (see Frynta *et al.* 2001). The degree of morphological differentiation among these species is relatively low and can be successfully distinguished only when advanced multivariate methods of skull morphometrics are employed (eg Janžeković and Kryštufek 2004 and those cited below). However, recent allozyme data suggest that individual *Sylvaemus* species are genetically well differentiated and maintain their genetic identity throughout their entire geographic ranges (Filippucci *et al.* 1989, Mezhzherin 1990, Mezhzherin and Zykov 1991, Filippucci 1992, Vogel *et al.* 1992, Filippucci *et al.* 1996, Mezhzherin 1997b, Macholán *et al.* 2001, Filippucci *et al.* 2002). No cases of obvious genetic introgression have been reported so far (but see Hille *et al.* 2002).

Evaluation of phylogenetic tree of *Sylvaemus* revealed no agreement among independent allozyme analyses, but DNA sequence data provide fairly congruent and reliable phylogenies (eg Chelomina *et al.* 1998, Martin *et al.* 2000, Michaux *et al.* 2002, Reuter *et al.* 2003, Bellinvia 2004). *A. hermonensis* Filippucci, Simson, and Nevo, 1989 represents the basal clade (Michaux *et al.* 2002, Reuter *et al.* 2003, Bellinvia 2004, in accordance with the earlier results obtained with RAPD technique: Bellinvia *et al.* 1999). *A. sylvaticus* (Linnaeus, 1758) forms the next offshot (but see Martin *et al.* 2000). According to Michaux *et al.* (2002), who examined two genes (12SrRNA and cytochrome b), the remaining species, ie *A. flavicollis, A. alpicola* Heinrich, 1952, and *A. uralensis* (Pallas, 1811), including *A. microps* Kratochvíl and Rosický, 1952, form the third distinct clade of the *Sylvaemus* group. Bellinvia (2004), who examined the control region (D-loop) of mt DNA of several *Sylvaemus* species/populations (some of them were identical to our samples), supports the close relationships among *A. flavicollis*, *A. alpicola* and *A. uralensis*. Moreover, she suggests the following relationships within this clade: (a) sister relationships between *A. alpicola* and *A. flavicollis*; (b) considerable differences (on subspecific level) between populations of *A. flavicollis* from Near East and Europe (see also Michaux *et al.* 2004); (c) close relationship between *Apodemus* sp. sample from Kirghyzstan and *A. uralensis* from Central Europe and Anatolia; and (d) clear distinction but uncertain position of *A. hyrcanicus* (possibly sister species of either *flavicollis-alpicola* clade or alternatively *A. uralensis*).

Individual *Apodemus* species and/or populations and especially those in the *Sylvaemus* clade occupy various habitats from open steppe to lowland mountain forest, and consequently they are likely to be exposed to different selective pressures associated with these environments. Their habitat preferences are usually species-specific – *A. flavicollis* (eg Steiner 1968, Montgomery 1978, Marsh and Harris 2000) and *A. hyrcanicus* (our data, Vorontsov *et al.* 1992) are consistently forest dwellers, *A. sylvaticus* is most abundant in ecotones and shrubs (eg Zejda 1965, Steiner 1968, Čiháková *et al.* 1993, Frynta *et al.* 1994), *A. hermonensis* regularly inhabits open habitats including alpine zones, steppes and semideserts (Filippucci *et al.* 1989, 1996, Macholán *et al.* 2001, D. Frynta, P. Mikulová and V. Vohralík, unpubl.). Less frequently distant populations of a single species exhibit different habitat requirements, eg *A. uralensis* in Central Europe is mostly confined to fields (eg Kratochvíl 1962, Stanko 1994) while the same species is restricted to forests in Anatolia (Macholán *et al.* 2001). Even when the habitat preferences are identical, different populations might be subjected to different selective pressures as a result of local environmental (eg climatic and landscape) and ecological (eg diverse muroid rodent assemblages) conditions. Therefore, we expect that some species and/or populations of the genus *Apodemus* have been subjected to rapid adaptive morphological evolution capa-

ble of outweighing the phylogenetic signal. The question is whether some traits evolved in such an adaptive manner or, alternatively, were subjected to non-adaptive processes (eg a gradual morphological evolution coinciding with the molecular variation). Corroborated phylogenetic hypotheses and extensive knowledge of *Apodemus* ecology and general biology provide an opportunity to use *Apodemus* morphology as an appropriate evolutionary model.

Up to now, a morphometric analysis that includes a more complete set of species and/or populations has not been undertaken yet. Previous multivariate morphometric studies were restricted to a limited subset of species or geographic areas, eg the Alps (Reuter *et al.* 1999), Italy (Filippucci *et al.* 1984, Panzironi *et al.* 1994), Bulgaria (Popov 1993), Turkish Islands (Özkan and Kryštufek 1999), Daghestan (Lavrenchenko and Likhnova 1995), Near East (Frynta *et al.* 2001), and consequently, they do not allow direct comparison between morphometric evolution and phylogeny.

The aim of this study is to: (1) analyse morphometric variation of cranial and dental characteristics in the majority of *Apodemus* species of the Western Palaearctics; (2) assess intra- and interspecific components of this variation; (3) compare morphometric results and existing phylogenetic relationships and (4) discuss possible causes underlying determinants of observed morphometric differentiation.

Material and methods

The majority of European *A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. agrarius* and *A. epimelas* as well as all *Apodemus* from Near East were collected by D. F., V. V. and colleagues during field studies in the Czech Republic and expeditions to the Balkans (1977–1999) and Middle East (1989–2001). These specimens have been deposited in the collections of the Department of Zoology, Charles University in Prague. Other specimens were provided by the National Museum in Prague (majority of *A. agrarius*, *A. uralensis* from Kirghyzstan) and Institute of Vertebrate Biology of the Czech Academy of Sciences in Brno (majority of European *A. uralensis*).

Mice were wild caught or they were of the first generation (except the control *A. sylvaticus* sample). Taking into account, that age may affect both size and shape, we decided to restrict our analyses just to fully grown animals. Although laboratory studies suggest that the growth of wood mice is indeterminate, the growth rates are fairly small in aged animals (see Frynta and Žižková 1992). Thus we included only the individuals of high abrasion category (mostly category 4 and 5 *sensu* Steiner 1968 – all individuals of *A. sylvaticus* and *A. flavicollis* populations from Central Europe; of *A. epimelas*, *A. agrarius*, *A. sylvaticus*, *A. flavicolllis* populations from Balkans; of *A. uralensis* population from Kirghyzstan) or we kept individuals in captivity for several months until they approached their asymptotic size (some field trapped individuals or individuals of first captive born genaration of *A. mystacinus*, *A. hermonensis*, *A. hyrcanicus*, *A. flavicollis*, *A. uralensis* population from Near East and of *A. agrarius*, *A. uralensis* populations from Central Europe). This procedure enabled us to rule out the effect of growth while the size component of the variation remained unchanged in the analyses. To evaluate morphological changes in captive-born individuals we also included sample of *A. sylvaticus* from laboratory colony with individuals of first, second and third generation (further referred as control population) in our analyses.

Altogether, we investigated 501 specimens of the following 9 species:

Apodemus uralensis: Central Europe – 44 specimens from the Czech Republic (southern Moravia: Dyjákovičky 15, Podvorov 3, Lužice 6, Čejkovice 7, Dubňany 2, Lednice 3, Zaječí 1, Dolní Bojanovice 1, M. Žižkov 2, Bavory 2, Vranovice 1, Dolní Dunajovice 1); Near East – 38 specimens from eastern Turkey (Seyfe 10, Güzyurdu 2, Yalnizcam Geçidi 5, Bağdaşan 3, Damar 8, Kabaca 8), Armenia (surroundings of Erevan 1) and Azerbaijan (Zakataly Reserve 1); Kirghyzstan – 29 specimens from Osh area.

Apodemus hermonensis: Near East – 52 specimens from eastern Turkey (Seyfe 1, Güzyurdu 4, Yalnizcam Geçidi 1, Bağdaşan 4, Aydoğlu 1, Damar 1, Kabaca 2, Sirbasan 8) and Iran (Vali Abad 3, Gholaman 7, Yasuj 13, Abshar 2, Sivand 1, Shiraz 4). Note: recently, Kryštufek (2002) suggested the use of the oldest available synonym *A. iconicus* Heptner, 1948.

Apodemus flavicollis: Central Europe – 36 specimens from the Czech Republic (Prague); Balkans – 75 specimens from Bulgaria (Gorna Breznica 23, Knižovnik 3, Kresna 2, Krumovo 1, Zornica 1), northern Greece (Kato Vermion 2, Kastania 11, Rentina 4, Nea Mechaniona 2, Kalivia 11, Stavropouli 7, Agios Ioannis Prodromos 5, Sminthi 2 and Thassos 1); Near East – 15 specimens from Armenia (surroundings of Erevan 3), eastern Turkey (Güzyurdu 1, Kabaca 1), Iran (Gholaman 9) and Syria (Slinfeh 1). Note: some authors suggest that *flavicollis*-like populations from the neighbouring Transcaucasus region belong to the distinct species *A. ponticus* Svirindenko, 1936 (cf Mezhzherin 1991, 1997a).

Apodemus cf. *hyrcanicus*: Near East – 29 specimens from Iran (Asalem 17, Now Kandeh 12). Note: *A. hyrcanicus* was described from the Hyrcanian Reserve in Azerbaijan (Vorontsov *et al.* 1992) approximately 80 km north of Asalem. Therefore, it is possible, that it is conspecific with other specimens from Iran (cf Macholán *et al.* 2001, Bellinvia 2004).

Apodemus sylvaticus: Central Europe – 37 wild-caught specimens from the Czech Republic (Prague), 38 specimens from the laboratory colony (established from wild animals captured in Prague) of first, second or third generation. This group was used as a control for comparison with previ-

ous group. Balkans – 16 specimens from Bulgaria (Gorna Breznica 10, Knižovnik 3, Arda1) and Greece (Langadas 1, Maronia 1).

Apodemus mystacinus: Near East – 29 specimens from Syria (Quanawat 17, Bloudan 3, Slinfeh 5) and Jordan (Ajlun 4).

Apodemus epimelas: Balkans – 26 specimens from Bulgaria (Gorna Breznica).

Apodemus agrarius: Central Europe – 27 specimens from Slovakia (Vihorlat Mts. 13, Kapušany 8, Belá 1, Ruská Poruba 1) and the Czech Republic (Broumov 2, Opava 1, Liberec 1), Balkans – 8 specimens from Bulgaria (Iskra 2, Petrič 1, Sandanski 1) and Macedonia (Skopje 3, Strumica 1).

Apodemus peninsulae: 4 specimens from Russian Far East (in the vicinity of Vyazemskiy, district Khabarovsk).

For schematic map of the studied localities see Fig. 1; details of the localities are given in the following papers: the Balkans – Vohralík (1985); Vohralík and Sofianidou (1987, 1992a, b); the Near East – Frynta *et al.* (2001); Prague – Mikulová and Frynta (2001); *Karstomys* – Vohralík *et al.* (2002).

In order to evaluate intraspecific variation, we included samples from geographically distant populations (for phylogeography see Michaux *et al.* 2003, 2004, 2005), ie from the Central-Europe, the Balkans and the Near East.

Most of the *Sylvaemus* specimens from Near East were identified using genetic methods (allozymes, 78 specimens, Macholán *et al.* 2001) or they were descendants of identified individuals (for list of these specimens see Frynta *et al.* 2001). The species identity of other specimens from Near East was assigned according to the discriminant function analysis based on skull and body measurements (Frynta *et al.* 2001). Specimens from Kirghyzstan were identified as *A. uralensis sensu lato*, since it is the only *Apodemus* to inhabit that region (Mezhzherin 1997a). Our decision was confirmed by sequencing the control region (D-loop) of mtDNA (Bellinvia 2004).

Identification of *A. sylvaticus* and *A. flavicollis* from the Balkans was based on the position of posterior edges of foramina incisiva in relation to the anterior roots of M^1 (Filippucci *et al.* 1984, Popov 1993) and on the allometry between facial length and length of foramen incisivum (Tvrtković 1979, Kryštufek and Stojanovski 1996).

The skulls were cleaned using *Dermestes* larvae. Thirteen cranial characters were measured using callipers with an accuracy of 0.1 mm (9 characters) or stereomicroscope to the nearest 0.05 mm (FI, PAL, BULL) or 0.014 mm (MZ), for details see Frynta *et al.*, 2001: CBL – condylobasal length, FL – facial length, ZYG – zygomatic breadth, RW – rostral width (maximum distance), IOW – interorbital width (minimum distance), BCW – brain-case width, IBW – interbullar width (shortest distance between left and right porus acusticus externus), RH – rostral height, BCH – brain-case height, FI – length of foramen incisivum, PAL

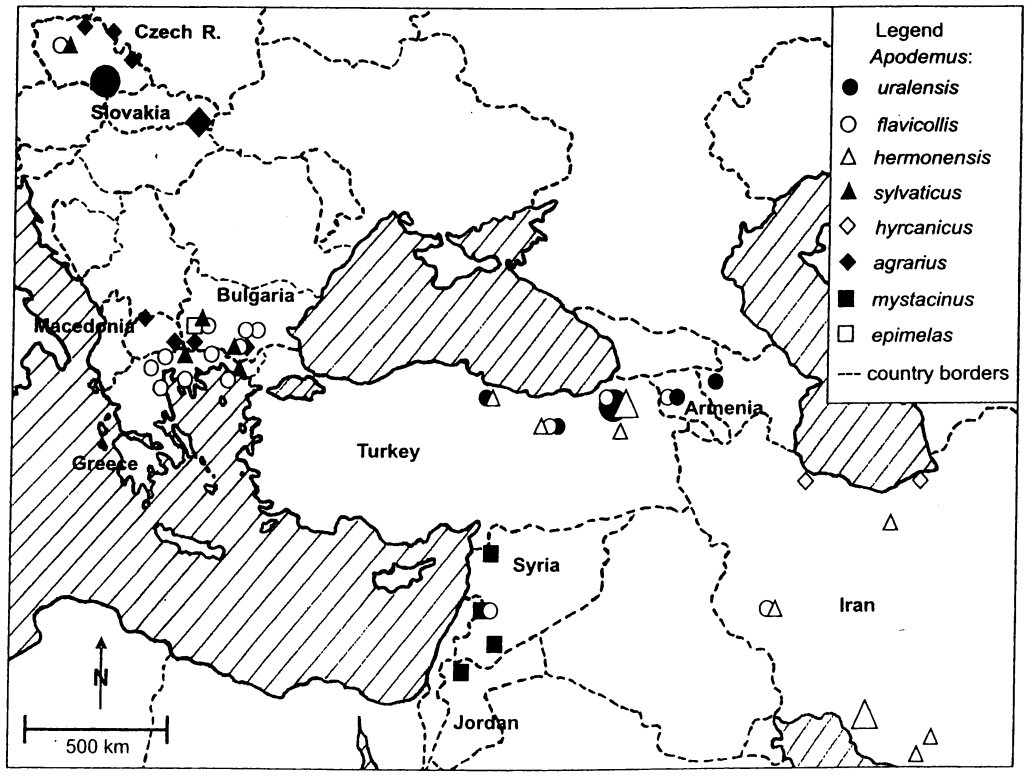

Fig. 1. Schematic map of the studied localities. Russian Far East (*A. peninsulae*) and Kirghyzstan (*A. uralensis*) are not depicted. Bigger sizes of symbols indicate more than one important localities where larger number of animals were collected.

– palatal length, BULL – bulla length and MZ – width of choanae. We used a stereomicroscope to obtain the following eight dental measurements (molars measured on the crowns as maximal distances): UML – upper molar row length (to the nearest 0.025 mm), RM^1L – first right upper molar length, RM^1W – first right upper molar width, RM^3L – third right upper molar length, RM^3W – third right upper molar width, RM_1L – first right lower molar length, RM_1W – first right lower molar width, INCW – upper incisor width (measured from the side view below os incisivum) (to the nearest 0.014 mm). Molar abrasion was assessed using a stereomicroscope following Steiner (1968).

The software STATISTICA Analysis System (release 6.0) was used for most calculations. We tested the data for normality prior to the statistical analyses. Deviations from normality were small, and most distributions were both unimodal and symmetrical as required for multivariate procedures.

The data were log-transformed and missing values were replaced with those predicted from regression analyses using condylobasal length or length of the first upper molar for tooth measurements as an independent variables. Each population was treated separately. To rule out the effect of growth and size, two different methods were used: (1) the Mosimann method of size adjustment (Mosimann 1970), in which the generalised size of each specimen has been calculated as the mean of log – transformed variables included in the analysis and each particular log-transformed measurement (natural logarithm) was standardised by subtracting the general size of the specimen or (2) residuals from regression on PC 1 (Burnaby 1966). These data sets are hereafter referred to as size-free. ZYG was omitted in size-free analyses to comply with software requirements.

Both the log-transformed and size-free data were used for computing squared Mahalanobis distances (under the Discriminant Analysis subroutine of the STATISTICA) among all 16 samples. UPGMA (STATISTICA) clustering was used to construct phenetic trees.

Next, we performed Discriminant Function Analyses (DFA) and Canonical Analysis for all *Sylvaemus* species (11 populations/samples). Scores of the first two canonical roots were used to visualise morphometric relationships between *Sylvaemus* populations in a biplot. The next axes (Root 3 and higher ones) were not suggested due to their low explanatory values (eigenvalues approached (Root 3) or dropped below the critical value 1).

Results

Genus *Apodemus*

Phenetic comparisons based on log-transformed data (see Appendix 1 for matrix of squared Mahalanobis distances, and Fig. 2 for

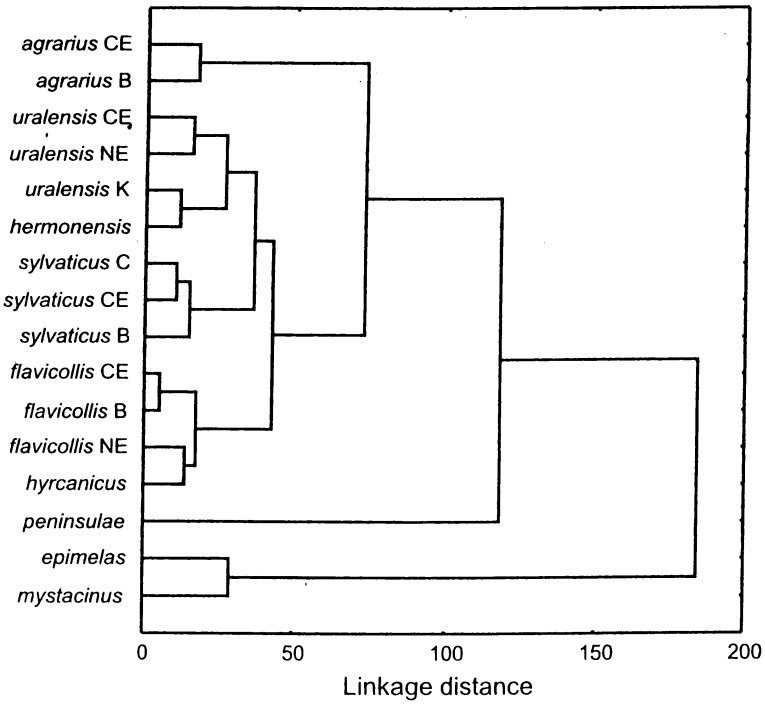

Fig. 2. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from original log-transformed data. Sixteen samples belonging to 3 subgenera were processed (*Apodemus*: *A. agrarius*, *A. peninsulae*; *Karstomys*: *A. epimelas*, *A. mystacinus*; *Sylvaemus*: *A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. hermonensis*, *A. hyrcanicus*). CE – Central Europe, B – Balkans, NE – Near East, K – Kirghyzstan, C – laboratory colony.

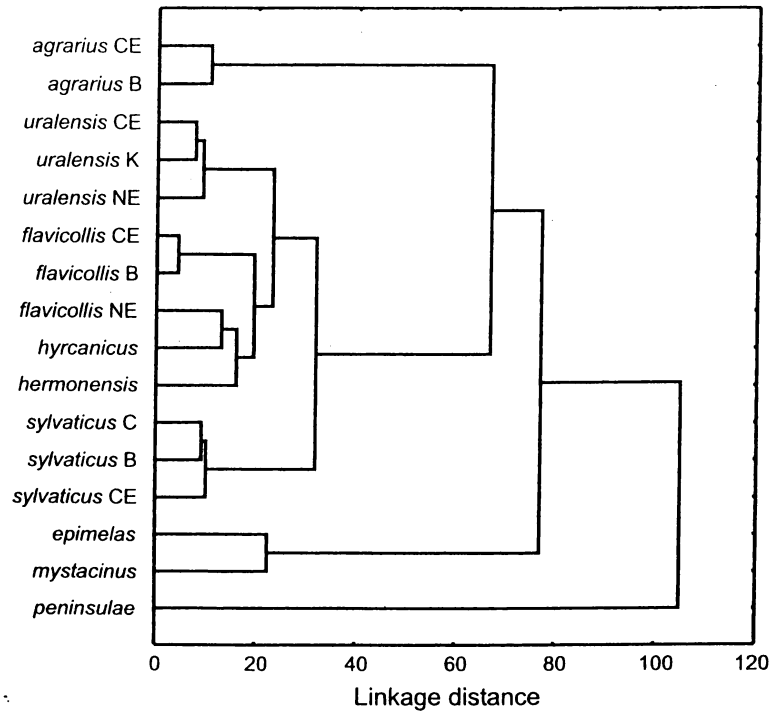

Fig. 3. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from size – adjusted data by using the Mosimann method. Sixteen samples belonging to 3 subgenera were processed (*Apodemus*: *A. agrarius*, *A. peninsulae*; *Karstomys*: *A. epimelas*, *A. mystacinus*; *Sylvaemus*: *A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. hermonensis*, *A. hyrcanicus*). CE – Central Europe, B – Balkans, NE – Near East, K – Kirghyzstan, C – laboratory colony.

UPGMA tree) revealed clear distinctions of subgenera *Karstomys* (with most basal position), *Apodemus* (two subsequent branches) and *Sylvaemus* (terminal position). Moreover, multiple samples of a single species clustered according to their species identity. Samples in the subgenus *Sylvaemus* formed three groups: *flavicollis-hyrcanicus* (branching first), *sylvaticus* and *uralensis-hermonensis*. *A. hyrcanicus* clustered with *A. flavicollis* from Near East and *A. hermonensis* with *A. uralensis* from Kirgyzstan.

Next, we repeated the above analyses using data from which size component was subtracted. Data that were size-adjusted by using Mosimann method (see Appendix 1 for matrix of squared Mahalanobis distances, and Fig. 3 for UPGMA tree). The resulting tree supported the distinctiveness of the *Sylvaemus* and *Karstomys* subgenera; the latter clustered within species of the *Apodemus* subgenus. Within *Sylvaemus*, *A. sylvaticus* represented the basal branch and the remaining samples formed a *uralensis* group and a *flavicollis-hyrcanicus-hermonensis* group, respectively. Nevertheless, the position of *A. hermonensis* was sensitive to the clustering method used, eg, single Linkage placed it again into *A. uralensis* cluster.

The tree constructed from residuals on PC1 (see Appendix 1 for matrix of squared Mahalanobis distances, and Fig. 4 for UPGMA tree) differs from the previous one in the position of *Karstomys* (both species clustered within *Sylvaemus*). *A. hermonensis* clustered with *A. uralensis* from Kirgyzstan in congruence with trees constructed from size-in data.

Subgenus *Sylvaemus*

In order to evaluate detailed relationships among *Sylvaemus* species and/or samples, we

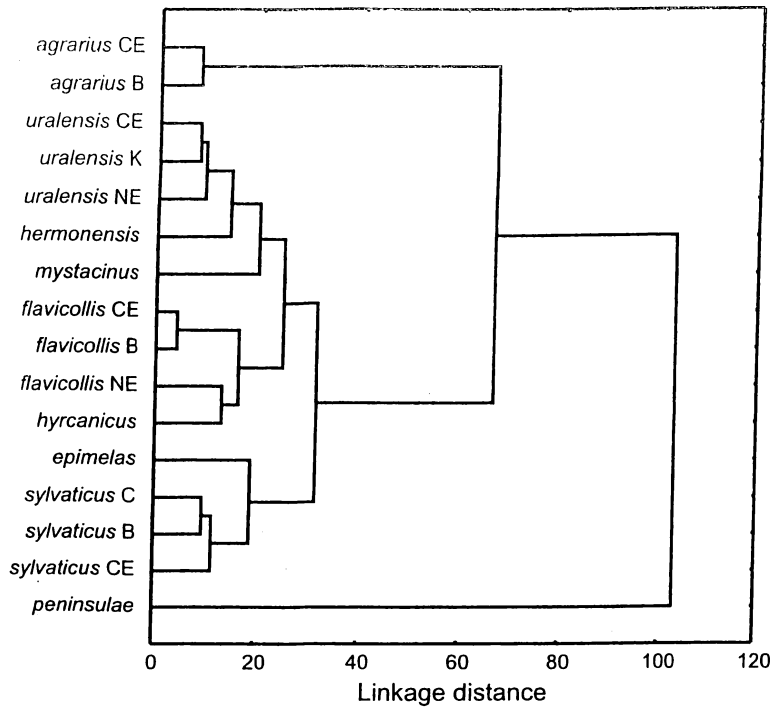

Fig. 4. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from residuals on PC 1. Sixteen samples belonging to 3 subgenera were processed (*Apodemus*: *A. agrarius*, *A. peninsulae*; *Karstomys*: *A. epimelas*, *A. mystacinus*; *Sylvaemus*: *A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. hermonensis*, *A. hyrcanicus*). CE – Central Europe, B – Balkans, NE – Near East, K – Kirghyzstan, C – laboratory colony.

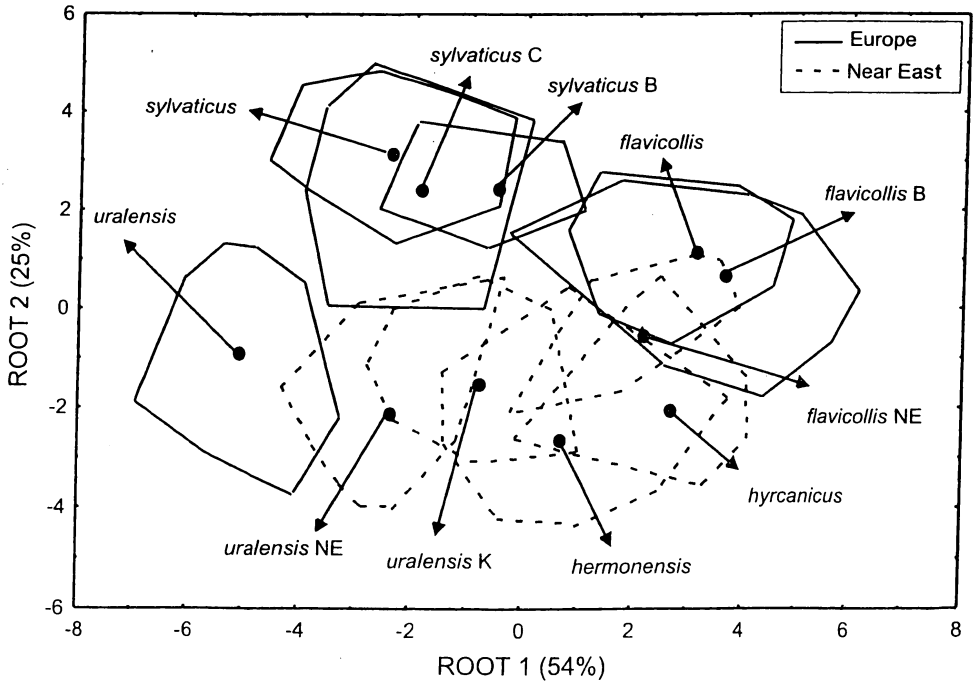

Fig. 5. Projection of 11 samples of five *Sylvaemus* species onto the first two canonical variates as derived from original log-transformed measurements. K – Kirghyzstan, C – laboratory colony, B – Balkans, NE – Near East. Solid circles depict sample means.

Table 1. Canonical variate loadings for 21 cranial and tooth measurements. Analysis based on original log-transformed data. See Material and methods for measurement abbreviations.

Cranial and tooth measurements	Root 1	Root 2
FI	0.255	0.525
UML	0.674	0.108
RM^1W	0.439	0.154
RM^1L	0.565	0.153
RM^3W	0.396	–0.001
RM^3L	0.413	–0.071
PAL	0.535	–0.398
RM_1L	0.504	0.152
MZ	0.215	–0.183
RM_1W	0.367	0.094
BULL	0.563	–0.017
INCW	0.538	–0.236
CBL	0.569	–0.158
FL	0.560	–0.152
RW	0.463	0.001
IOW	0.331	–0.136
BCW	0.455	–0.010
IBW	0.438	–0.079
RH	0.390	–0.222
BCH	0.516	0.281
ZYG	0.462	–0.265

performed separate canonical analyses of samples belonging to this subgenus. The positions of individual samples in the morphospace of the first two canonical roots computed from size-in data are provided in Fig. 5 (for loadings see Table 1). *A. uralensis*, *A. sylvaticus* and *A. flavicollis* populations from Central Europe are well separated. The position of Balkan populations of *A. flavicollis* and *A. sylvaticus* resembled those of their conspecifics from Central Europe. In sharp contrast, Near East populations of *A. uralensis*, *A. hermonensis*, *A. hyrcanicus*, *A. flavicollis* as well as *A. uralensis* from Kirghyzstan were situated within the triangle formed by the European species and tend to overlap each other. Comparable analyses carried out using size-free data produced fairly similar patterns (residuals from PC1 – Fig. 7, for loadings see Table 3; data adjusted using the Mosimann method – Fig. 6, for loadings see Table 2) with species/populations being more compressed with each other.

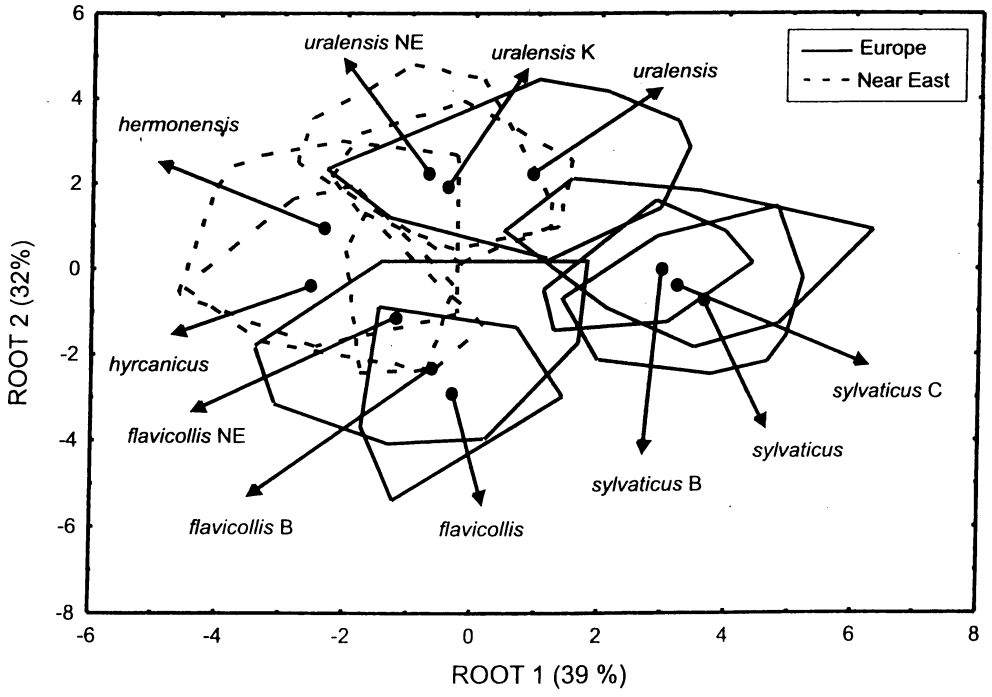

Fig. 6. Projection of 11 samples of five *Sylvaemus* species onto the first two canonical variates as derived from from size – adjusted data by using the Mosimann method. K – Kirghyzstan, C – laboratory colony, B – Balkans, NE – Near East. Solid circles depict sample means.

Table 2. Canonical variate loadings for 20 cranial and tooth measurements. Analysis based on data adjusted by using the Mosimann method. See Material and methods for measurement abbreviations.

Cranial and tooth measurements	Root 1	Root 2
FI	0.670	–0.085
UML	0.101	–0.290
RM^1W	0.298	0.022
RM^1L	0.119	–0.275
RM^3W	–0.040	–0.143
RM^3L	–0.123	–0.115
PAL	–0.478	–0.014
RM_1L	0.167	–0.193
MZ	–0.193	0.009
RM_1W	0.254	0.093
BULL	–0.106	–0.260
INCW	–0.333	–0.119
CBL	–0.014	0.250
FL	–0.008	0.258
RW	–0.004	–0.103
IOW	0.079	0.310
BCW	0.340	0.428
IBW	0.135	0.290
RH	–0.118	0.233
BCH	0.396	–0.089

Table 3. Canonical variate loadings for 20 cranial and tooth measurements. Analysis based on original residuals on PC1. See Material and methods for measurement abbreviations.

Cranial and tooth measurements	Root 1	Root 2
FI	–0.642	–0.351
UML	–0.214	0.010
RM^1W	–0.232	–0.098
RM^1L	–0.227	0.061
RM^3W	–0.028	0.071
RM^3L	0.048	0.016
PAL	0.427	0.116
RM_1L	–0.235	–0.074
MZ	0.142	–0.132
RM_1W	–0.174	–0.210
BULL	0.041	0.610
INCW	0.251	0.241
CBL	0.184	–0.074
FL	0.170	–0.147
RW	0.005	0.347
IOW	0.129	–0.011
BCW	–0.062	–0.290
IBW	0.060	–0.095
RH	0.235	–0.138
BCH	–0.373	0.111

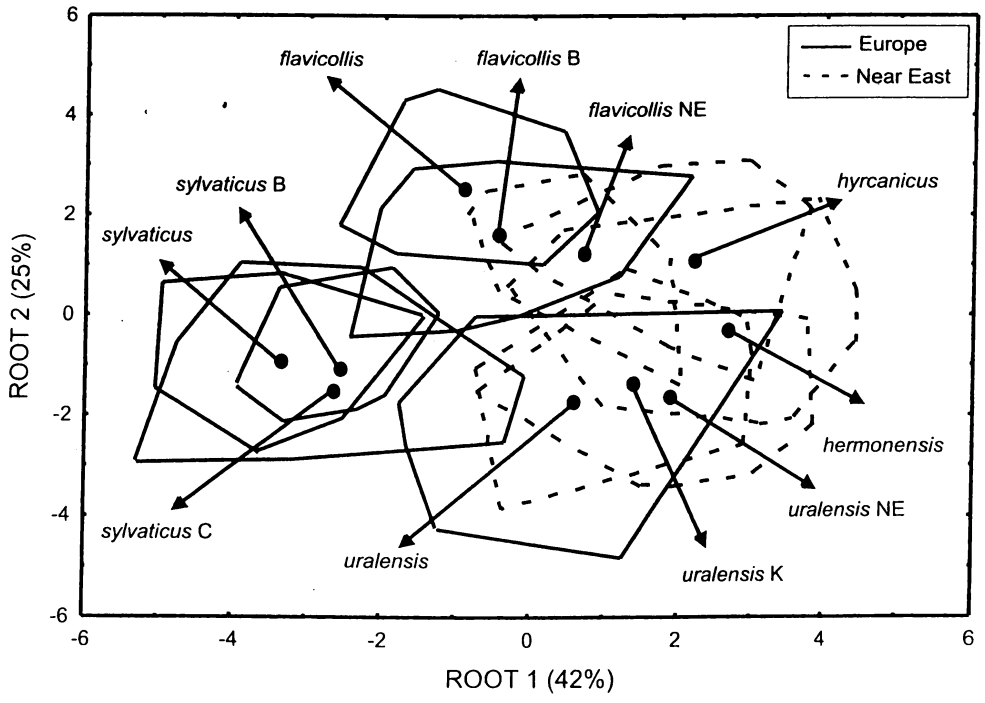

Fig. 7. Projection of 11 samples of five *Sylvaemus* species onto the first two canonical variates as derived from residuals on PC 1. K – Kirghyzstan, C – laboratory colony, B – Balkans, NE – Near East. Solid circles depict sample means.

Discussion

The phenetic trees based on size-in (log-transformed) and size-free (Mosimann method, residuals on PC1) data reveal a similar branching pattern. This pattern is more or less congruent with current phylogenetic hypotheses.

As expected, species of the *Apodemus* subgenus tend to maintain basal position and those of the *Sylvaemus* subgenus form a single cluster. However, the position of the subgenus *Karstomys* was highly dependent on the computation method: size-in analysis placed this subgenus on the tree base, while the size-free method based on residuals on PC1 placed it within the *Sylvaemus* subgenus. These dichotomous results may be attributed to the large body size of *Karstomys* species. It is not surprising that including the size component into the analysis of morphometric distances may affect the position of species that exhibit extreme body sizes. In contrast, explanation of the latter case is less trivial. There is a potential problem with estimation of interspecific allometric relationships in taxa with biased distribution of body size. The slope of linear least-square regression line is heavily influenced by outstanding points (those far from the main cluster). The value of residuals in species with extreme body size may be consequently shifted to zero. This explanation is indirectly supported by the distinct position of the *Karstomys* subgenus in the other size-free analysis (Mosimann) corrected for isometric growth.

Morphometric distances between *A. epimelas* and *A. mystacinus* are comparable to those found between traditionally recognized *Sylvaemus* species. Thus, their elevation from a subspecies to a species level seems to be supported (Mezhzherin 1997a, Vohralík *et al.* 2002, Bellinvia 2004, Michaux *et al.* 2005).

Most surprising was the clustering of samples within the subgenus *Sylvaemus*. In spite of a high level of morphological similarity among species and substantial differences in local ecological conditions to which individual populations are exposed, samples representing a single species clustered together in most cases. Moreover, the sister relationship between the *A. flavicollis* (possibly including *A. hyrcanicus*) and *A. uralensis* groups, as well as more basal position of *A. sylvaticus* as suggested by molecular data (Bellinvia 2004), were clearly supported by morphometric analyses of size-free data. In size-in analysis, however, body size was more important than the shape component and, consequently, the *A. flavicollis* group (including *A. hyrcanicus*) clustered separately from the remaining *Sylvaemus* species which share smaller body sizes. Interestingly, our morphometric results support also the phylogeographic subdivision of *A. flavicollis* into the Near East and European branch, recently presented by Michaux *et al.* (2004). The apparent discrepancy between sister relationship of *A. hermonensis* with the respect to remaining species of the subgenus *Sylvaemus* suggested by DNA phylogenies (Bellinvia *et al.* 1999, Bellinvia 2004), and morphometric similarity of this species to *A. uralensis* and/or *A. hyrcanicus–A. flavicollis* may suggest that this species has conserved more ancestral phenotype than *A. sylvaticus*. The latter species probably underwent a rapid evolution as also evident from high values of phenetic distances between *A. sylvaticus* and other *Sylvaemus* reported by allozyme studies (Macholán *et al.* 2001).

Above mentioned congruence between morphometric and phylogenetic trees is surprising, nevertheless, it has been reported previously, eg in the genus *Mus* (Macholán 2001). Such a concordance may suggest that the evaluated morphometric traits exhibit phylogenetic conservatism and therefore are not completely determined by selective pressures and corresponding episodes of adaptive evolution.

Besides the phylogenetic pattern, there is also a subtle, but remarkable, morphometric divergence on a regional scale. We found that European species of the subgenus *Sylvaemus* are well separated in a morphospace (most apparently in size-in analysis), while those inhabiting the Near East occupy an intermediate position and overlap with each other. Moreover, the same trend can be demonstrated within a particular species. When *A. flavicollis* or *A. uralensis* from both regions are compared, the Near East populations are somewhat shifted towards other species/populations in this region.

The observed phenomenon cannot be attributted to phylogeny itself because, neither European nor Near East assamblage of *Sylvaemus* taxa represents an exclusive clade (Bellinvia *et al.* 1999, Bellinvia 2004). The possible explanations are (1) gene introgression among sympatric species in the Near East and/or (2) convergent evolution of multiple clades in the Near East and/or (3) divergent evolution in European taxa combined with persistence of ancestral phenotypes in the Near East.

The first scenario may be ruled out because all *Sylvaemus* species maintain their genetic identity throughout their entire geographic ranges (Filippucci *et al.* 1989, Mezhzherin 1990, Mezhzherin and Zykov 1991, Filippucci 1992, Vogel *et al.* 1992, Filippucci *et al.* 1996, Mezhzherin 1997b, Macholán *et al.* 2001, Filippucci *et al.* 2002). When considering the second and the third scenario we bear following facts in mind. Divergent evolution (third scenario) may be caused by almost every evolutionary mechanism, while conditions for convergent evolution (second scenario) are more restrictive – it requires similar selective pressures (or constraints) operating in populations of different taxa. Nevertheless we have no direct evidence in favour of divergent (more probable) or convergent scenario, so we futher discuss both above mentioned alternatives equally.

Convergence/divergence may be caused by adaptive (genetic and/or phenotypic plasticity cf West-Eberhard 1989, 2003) as well as non-adaptive processes (genetic drift etc.). Although having no direct evidence, we consider the adaptive cause more probable (adaptation is directional as it seems to be the morphological change).

Putative selective pressures influencing the direction and degree of adaptive morphological changes can be a result of ecological (eg diverse muroid rodent assemblages) or local environmental (eg climatic and landscape) conditions. Divergence due to character displacement is an unlikely explanation. In Europe, the sympatric occurrence of *A. flavicollis* and *A. sylvaticus* (eg Marsh and Harris 2000) as well as *A. uralensis* and *A. sylvaticus* is frequently reported and sometimes all three species can be found together (Spitzenberger and Steiner 1967, Obrtel and Holišová 1983). However, in Central Europe we failed to demonstrate character release in *A. sylvaticus* occupying localities where *A. flavicollis* is absent (Mikulová and Frynta 2001). Although we did not analyse mice from sympatric and allopatric populations separately, it is evident, that at least in some regions of the Near East, two or even three morphologically similar *Sylvaemus* species occur in closer sympatry (without visible separation on microhabitat scale) than in Europe (*A. hermonensis*, *A. flavicollis* and *A. uralensis* in the northern part of Anatolia or *A. hermonensis* and *A. flavicollis* in the Zagros Mts; Filippucci *et al.* 1996, Frynta *et al.* 2001, Macholán *et al.* 2001). On the other hand, our samples from Kirghyzstan and from the Hyrcanian forests along the Caspian Sea represent only a single species (*A. uralensis* and *A. hyrcanicus*, respectively).

We can only speculate about possible ecological causes of small interspecific variation in the Middle East when compared to that in Europe. Obviously, habitats suitable for the survival of *Sylvaemus* species are more differentiated in European landscapes (field - shrub - forest) than in the Near East, where both margins of this habitat scale are reduced as consequence of arid climate and deforestation. Moreover, fields are often densely inhabited by other seed eating rodents, such as *Mus macedonicus* and/or *Mus domesticus* in the Near East. Consequently, adaptive zones of Near East taxa may be correspondingly reduced and potentially resulting in enhanced morphological similarity among the Near East *Apodemus* species.

This finding is not easily interpreted in the terms of performance (sensu Garland 1994) because the morphometric differences among *Sylvaemus* populations are generally subtle, of a multivariate nature (comprising size as well as shape component, but no single trait interpretable in functional context) and appropriate characteristics (behaviour, performance) of studied taxa are not available. Moreover, our explanation of the adaptive variation is based solely on present ecological conditions. The landscapes of the Western Palaeartics have undergone considerable changes since the divergence of *Sylvaemus*, which was estimated to 850 000

and 1–1.5 Myr BP on the basis of the Nei genetic distances (Filippucci *et al.* 1996, Mezhzherin 1997b, respectively) or 2 – 4 Myr BP based on DNA sequence divergence (Serizawa *et al.* 2000, see also Michaux *et al.* 2002). Unfortunately, there is a significant absence of relevant data that would allow us to assess the relationship between skull morphometrics and landscape ecology during the course of history.

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V.

Ecomorphology of the genus *Apodemus* (Muridae: Rodentia): morphometry of postcranial skeleton

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Submitted for publicatin

Abstract

We studied skeletons of 265 wood mice belonging to eight species from Europe and Near East: *A. agrarius*, *A. mystacinus*, *A. hyrcanicus*, *A. hermonensis*, *A. uralensis* (=*microps*), *A. flavicollis* and *A. sylvaticus*. Thirty five postranial and body measurements were obtained and treated with multivariate statistics. The multivariate analysis, based on size adjusted data, revealed clear morphological differentiation among studied taxa. *A. (Apodemus) agrarius*, *A. (Karstomys) mystacinus* and *Sylvaemus* species formed clearly separated clusters in morphospace along the first and second canonical axes. Within subgenus *Sylvaemus*, the *A. sylvaticus* revealed morphological separation from other taxa of this subgenus along second canonical axis. The main differentiation of *Sylvaemus* species however took place along the third canonical axis. The contribution of phylogenetic conservatism and ecological strategies of studied species (in terms of above/under ground activities as digging, climbing, running etc) to observed morphological pattern is discussed.

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Key Words: morphometrics, performance, wood mice, *Sylvaemus, Karstomys.*

Introduction

Muroid rodents (family Muridae) represent highly diversified mammalian clade inhabiting nearly all habitat types. Consequently, individual rodent species exhibit specific adaptations to their way of life which may comprise behaviour (adaptive profile: Dewsbury *et al.* 1982), locomotory performance (*sensu* Garland 1994) and morphology (eg Price 1993). Closely related rodent taxa exhibiting different ecological and behavioural strategies, as eg wood mice of the genus *Apodemus* Kaup, 1829, may serve as a proper model for understanding these adaptive processes.

Wood mice are common murid rodents in the Palaearctic region (cf. Musser *et al.* 1996, Mitchell-Jones *et al.* 1999) where they fill the same adaptive zone as the genus *Peromyscus* in North America (Montgomery 1989). All the *Apodemus* species are opportunistic seed eaters consuming also insects and diverse additional vegetable components (eg Mirić 1966, Holišová 1967, Holišová and Obrtel 1977, 1980, Babinska-Werka 1981, Obrtel and Holišová 1983, Gebczynska *et al.* 1987, Montgomery and Montgomery 1990, Heroldová 1994, Rogers and Gorman 1995). They share generalized muroid morphology and exhibit high phenotypic similarity between species (eg Frynta *et al.* 2006), however, individual *Apodemus* species/populations differ in their preferred habitats and behaviour.

Species of the genus *Apodemus* inhabiting Europe, North Africa and Western Asia form three distinct clades (Musser *et al.* 1996, for genetic support see eg Martin *et al.* 2000, Michaux *et al.* 2002, Bellinvia 2004) corresponding to traditionally recognized subgenera: *Apodemus* Kaup, 1829, *Karstomys* Martino, 1939 and *Sylvaemus* Ognev, 1924.

Apodemus agrarius (Pallas, 1771), belonging to the East Asian subgenus *Apodemus,* is least related to the other wood mice species of the western Palaearctics. It has only recently (early Holocene) extended its range from the Far East westwards to Europe (Böhme 1978). *A. agrarius* is predominantly field-dweller associated with crop-fields, grasslands, and open wet habitats, especially along the rivers and streams (Kratochvíl 1962, 1977, Zejda 1967, Karaseva *et al.* 1992).

Karstomys consists of only two species: *A. epimelas* (Nehring, 1902) from the Balkans and *A. mystacinus* (Danford et Alston, 1877) from the Island of Crete and the Near

East (see Vohralík *et al.* 2002). Both these species are specialised rock-dwellers and represent the biggest forms of the genus *Apodemus*.

The subgenus *Sylvaemus* contains at least six species. Three of them *A. flavicollis* (Melchior, 1834), *A. sylvaticus* (Linnaeus, 1758) and *A. uralensis* (Pallas, 1811), including *A. microps* Kratochvíl and Rosický, 1952, are traditionally recognised and represent the most morphologically differentiated forms of the subgenus (Steiner 1968, Frynta *et al.* 2006). In the Central Europe, they exhibit contrasting ecological strategies. *A. flavicollis* is forest-dweller (eg Steiner 1968, Montgomery 1977, Marsh and Harris 2000), *A. uralensis* field-dweller (eg Kratochvíl 1962, Stanko 1994), and *A. sylvaticus* exhibits less specialised requirements reaching its maximal abundance in ecotones including forest margins, bushes, set aside fields, parks, etc (eg Zejda 1965, Steiner 1968, Čiháková *et al.* 1993, Frynta *et al.* 1994). These preferences were clearly supported by a study of rodent assamblages in windbreaks and adjacent fields performed in Southern Moravia (Central Europe; Pelikán 1986).

While the habitat requirements of European species were studied in detail (see above), only fragmentary information is available for the *Sylvaemus* species of the Near East. *A. hyrcanicus* Voronstov, Boyeskorov, Mezhzherin, Lyapunova, and Kandaurov, 1992, only recently recognised form from the Hyrcanian area along the Caspian Sea, is obviously confined to forest (our data, Vorontsov *et al.* 1992). Populations of the other species *A. uralensis* (limited to the Northern Anatolia and Transcaucasus), *A. flavicollis* and *A. hermonensis* Filippucci, Simson, and Nevo, 1989 may be found even syntopically. Nevertheless, the *A. hermonensis* is the only species of this area regularly inhabiting steppes and/or semideserts, while the former two species are more or less restricted to forest and bushes (Filippucci *et al.* 1989, Filippucci *et al.*1996, Macholán *et al.* 2001, and our unpublished data).

Different habitat preferences described above may be associated with different locomotory performance. We can suppose that species living in open microhabitats (including forest/shrub habitats without dense undercover) should be better runners and jumpers than species able to live under dense grass cover (as eg *A. agrarius* Zejda 1967, Kratochvíl 1977). Some species inhabiting forest habitats are known to exhibit considerable arboreal activity (*A. flavicollis*: Borowski 1962, Holišová 1969, Montgomery

1980, Juškaitis 1995; *A. sylvaticus*: Montgomery 1980, Santos and Tellería 1991, Tattersall and Whitbread 1994 and references herein), and consequently should be more adapted to climbing. Finally, rock dwelling species (*A. mystacinus* and *A. epimelas*) and partly those able to use tree cavities instead of subterranean nests (*A. sylvaticus* and *A. flavicollis*) should be less adapted to digging.

There is, however, only limited information concerning locomotory performance of *Apodemus* species. When subjected to ten minute laboratory tests for exploratory behaviour (Frynta 1992, 1994), *Apodemus* species have split into three groups corresponding to subgenera. Among seven *Apodemus* species/subspecies included in this study, *A. epimelas* (the closest relative of *A. mystacinus)* exhibited the highest activity, while the representatives of the subgenus *Apodemus*, especially European population of *A. agrarius,* the lowest one. The species of the subgenus *Sylvaemus* have a fairly intermediate position. Jumping was correlated with activity scores (Frynta 1994). This behavioural element has never been recorded in European population of *A. agrarius* during the experiment. It was rare in *A. uralensis* (mean=0.4), and frequent in *A. flavicollis* (2.7), *A. sylvaticus* (4.0) and *A. epimelas* (7.9).

Considerable research effort, mostly for taxonomical and determination purposes, has been devoted to morphometric differences among *Apodemus* species (eg Filippucci *et al.* 1984, Popov 1993, Panzironi *et al.* 1994, Lavrenchenko and Likhnova 1995, Özkan and Kryštufek 1999, Reuter *et al.* 1999, Frynta *et al.* 2001). Therefore, the authors focused on cranial measurements that are usually supposed to be less affected by adaptive evolution. Recently, we analysed multivariate cranial morphometry of nine *Apodemus* species (16 samples, Frynta *et al.* 2006) and found a good correspondence between phenetic tree and current phylogenetic hypothesis based on DNA sequences (Michaux *et al.* 2002, Bellinvia 2004).

In contrast, only limited information is available about the morphological traits obviously associated with the way of locomotion. Attention has been paid only to some external measurements. The short tail, ear and hind-foot in *A. agrarius* may easily be attributed to high proportion of activity in burrows and tunnels in this species. The lengths of the tail, the hind-foot and the eye diameter have traditionally been considered by field workers to enable field determination of *Sylvaemus* species of similar appearance (Holišová

et al. 1962, Niethammer and Krapp 1978).

The length of vibrissae is functionally tight with the diameter of investigated space. Consequently, the subterranean species have usually short vibrissae, while those of rock-dwelling (petricolous) species are extremely long. Kratochvíl (1968) described vibrissae in five *Apodemus* species and found that their length increases sharply in the following order: *A. agrarius, A. uralensis, A. sylvaticus, A. flavicollis* and *A. mystacinus.*

This study is focused on postcranial skeleton measurements, to fulfil the nearly unstudied field of *Apodemus* morphology. These traits are likely associated with locomotory performance and are good candidates for adaptive evolution. High explanatory power of postcranial morphometry for understanding ecological strategy of a particular species may be, therefore, reasonably expected. The aim of our study is to (1) analyze morphometric variation of postcranial skeleton in the majority of *Apodemus* species of the Western Palaearctics, (2) assess intra- and interspecific component of this variation, (3) compare morphometric results and available phylogenetic relationships, (4) discuss ecological and behavioural correlates of observed differentiation.

Material and Methods

The material was collected by authors and their colleagues during field studies in the Czech Republic and Czech expeditions to Near East and Far East. All specimens are deposited in the collections of the Department of Zoology, Charles University in Prague. The studied mice were captured in the field or they were of the first captive-born generation. Some of the individuals (captured in the field as well as captive-born) were kept in captivity usually for several months in order to reach their asymptotic size, others were selected according to their molar abrasion (mostly category 4 and 5 *sensu* Steiner (1968)) and can be considered as fully grown (see Frynta and Žižková 1992 for the character of postnatal growth in *A. sylvaticus*). The only exception was the sample of *A. peninsulae* where age separation of the individuals was not used in size-free data (see bellow) due to a very small sample size and which therefore contains also two young individuals (molar abrasion of category 2). This procedure enabled us to rule out the effect of growth (except *A. peninsulae*) while the size component of the variation remained unchanged. Altogether, we studied 272

specimens belonging to the following eight species:

Apodemus uralensis: Central Europe – 23 specimens from the Czech Republic (southern Moravia: Dyjákovičky); Near East – 37 specimens from eastern Turkey (Seyfe 10, Güzyurdu 2, Yalnizcam Gecidi 4, Bagdasan 3, Damar 8, Kabaca 8), Armenia (surroundings of Erevan 1) and Azerbaijan (Zakataly Reserve 1).

Apodemus hermonensis: Near East – 49 specimens from eastern Turkey (Seyfe 1, Güzyurdu 4, Yalnizcam Gecidi 1, Bagdasan 4, Aydoglu 1, Damar 1, Kabaca 2, Sirbasan 9) and Iran (Vali Abad 2, Gholaman 7, Yasuj 12, Abshar 2, Sivand 1, Shiraz 2). Note: Recently, Kryštufek (2002) suggested to use the oldest available synonym *A. iconicus* (Heptner, 1948)).

Apodemus flavicollis: Central Europe – 31 specimens from the Czech Republic (Prague). Near East – 14 specimens from eastern Turkey (Güzyurdu 1, Kabaca 1), Iran (Gholaman 9) and Armenia (surroundings of Erevan 3).

Apodemus cf. *hyrcanicus*: Near East – 25 specimens from Iran (Asalem 15, Now Kandeh 10). Note: *A. hyrcanicus* was described from the Hyrcanian Reserve in Azerbaijan (Vorontsov *et al.* 1992) some 80 km north of one of our sites in Asalem. Its conspecificity with our material from Iran is thus probable, but not certain (Macholán *et al.* 2001).

Apodemus sylvaticus: Central Europe – 33 specimens from the Czech Republic (Prague)

Apodemus mystacinus: Near East – 31 specimens from Syria (Quanawat 17, Burqush 1, Slinfeh 12, Sarghaya 1).

Apodemus agrarius: Central Europe – 22 specimens from the Czech Republic (Opava 18, Krásná Lípa 4).

Apodemus peninsulae: 7 specimens from Russian Far East (the vicinity of the town Vyazemskiy, district Khabarovsk).

For details of the localities see the following papers: the Near East - Frynta *et al.* (2001); Prague - Mikulová and Frynta (2001); *Karstomys* - Vohralík *et al.* (2002).

Most of the studied *Sylvaemus* specimens from Near East were determined by biochemical methods (allozymes, 69 specimens, Macholán *et al.* 2001) or they were descendants of biochemically determined individuals (11 specimens). The localities Sirbasan, Now Kandeh and Asalem were treated as occupied by only one *Apodemus*

species, because all biochemically determined individuals from these localities belong to only one species. The species identity of other 18 specimens from Near East was assigned according to discriminant function analysis based on skull and body measurements (Frynta *et al.* 2001).

Standard external measurements of each individual were taken with the use of calliper: LCD- tail length, LC - body length (to the nearest mm), LTP – hind foot length and LA - ear length (to nearest 0.1 mm). Subsequently the skeletons were removed and biologically prepared using *Dermestes* larvae. 31 postcranial measurements were taken with the use of calliper: LH – length of humerus, LU – length of ulna, LP – length of pelvis, WP1- width of pars ischiopubica of os coxae, LT – length of tibia, LF – length of femur (to the nearest 0.1 mm) or under stereomicroscope: LS - length of scapula, WS1 - width of scapula (perpendicular to long axis of spina scapulae), LH1 – length of proximal part of humerus (to processus deltoideus), LT2 – length of dital part of tibia (from fusion of tibia with fibula), MET – length of corpus of third ossis metatarsalis (to the nearest 0.1 mm), SW2 width of os sacrum, VBW – width of sixth lumbal vertebra (on processii costarii), VBL – length of sixth lumbal vertebra, SW1 – distance between ossae coxae, WS2 - width of scapula (straight distance between angulus cranialis to angulus caudalis), OLE – length of olecranon (to incisura semilunaris), WH3 – width of distal part of humerus (from epicondylus lateralis to epicondylus medialis), LP2 – length of pars ischiopubica of os coxae, LSF – length of foramen obturatum, WSF – width of foramen obturatum (to the nearest 0.05 mm), WU – width of proximal part of ulna and radius, WH1- width of proximal part of humerus (including processus deltoideus), WH2 – width of distal part of humerus, WP2 – width of pars iliaca of os coxae , WF1 – width of proximal part of femur (including trochanter tertius), WF2 – width of distal part of femur, WF3 – width of collum femoralis, WF4 – distance between trochanter major and caput femoralis, WT1 – width of proximal part of tibia (including fossa laterale), WT2 – width of distal part of tibia and fibula (to the nearest 0.025 mm).

To avoid double using of the same measurements in our analyses LTP, LU, LH, LP, LH were used to obtain the following measurements: LTP1 (LTP minus MET) - lenght of tarsus and phalanges, LH2 (LH minus LH1) – length of distal part of humerus, LU1 (LU minus OLE)- length of distal part of ulna, LP1 (LP minus LP2) - length of pars iliaca of os

caxae (including fossa acetabularis) , LT1 (LT minus LT2)- lenght of proximal part of tibia (to the fusion of tibia and fibula). See Fig.1 for depiction of measurements used in our analyses and Appendix 1 for standard descriptive statistics of taken measurements .
The STATISTICA Analysis System (release 6.0) was used for most calculations. The data were checked for normality prior the statistical analyses, deviations from normality were small, and most distributions were both unimodal and symmetrical as required for the used multivariate procedures.

The data were log-transformed and missing ones were replaced by those predicted from regression using most correlated variable as an independent one (assessed according to correlation matrix of all variables). Each population was treated separately. To rule out the effect of growth and size, Mosimann method of size adjustment (Mosimann 1970) was used in some procedures. This data set is further referred to as "size-free". WS1 was omitted in size-free analyses to match software requirements.

Log-transformed data were treated by Principal component analysis (PCA). PC1, PC2, PC3 scores extracted for each individual were subjected to ANOVA in order to evaluate the variation amongst the studied samples.

Size-free data were used for computing squared Mahalanobis distances (under the Discriminant Analysis subroutine of the STATISTICA Analysis System) between all 10 *Apodemus* samples. UPGMA clustering (STATISTICA Analysis System) was used to construct phenetic tree.

Next, the size-free data for 9 *Apodemus* samples (excluding *A. peninsulae* due to small sample size) were subjected to Discriminant Function Analyses (DFA) and Canonical Analysis. Scores of the first three canonical roots were used to visualise morphometric relationships between samples in a biplot.

Classification function resulting from DFA analysis of studied samples was applied to individuals of *A. peninsulae* and computed scores of the first three canonical roots were used to visualise their position in morphospace according to other studied samples.

Results

Principal component analysis (PCA) of log-transformed data (for loadings see Tab 1)

revealed that PC1 explaining 71.7 % (eigenvalue = 25.1) of variance is highly and negatively correlated with all studied traits (r = 0.97 for femur length). Thus vast majority of variance in the data set can be attributed to the size component. Along the PC 1 axis, the studied species split into "large" (*A. mystacinus*), "medium" (*A. peninsulae*, *A. flavicollis* from both regions, *A. hyrcanicus, A. hermonensis*), and "small" (*A. uralensis* from Near East, *A. agrarius, A. sylvaticus*); *A. uralensis* from central Europe being the smallest one (Fig. 2). PC 2 axis (5.4 %, eigenvalue = 1.9) may be interpreted as relative size of distal elements (MET, LT2, LTP1) of the hind leg, foreleg (LU1, LH2), ear length (LA) and tail length (LCD), when compared with length of lumbal vertebra (VBL) and pelvis size (LSF, WP1, LP1). PC 2 axis clearly differentiates *A. agrarius* from remaining species that are further grouped as follows: (1) central European *A. uralensis*, *A. peninsulae, A. hermonensis, A. mystacinus,* (2) *A. uralensis* from Near East, *A. flavicollis, A. hyrcanicus* and *A. sylvaticus* (Fig. 3, note: post hoc tests revealed significant differences in following between group comparisons: *A. uralensis* CE vs *A. mystacinus*, *A. uralensis NE* vs *A. sylvaticus* and no significant differences in following between group comparisons *A. mystacinus* vs *A. flavicollis* NE, *A. hyrcanicus* and *A. uralensis* NE, *A. hermonensis* vs *A. flavicollis* NE). Finally, PC 3 axis (3.7 %, eigenvalue = 1.3) is positively correlated with pelvis width (WP2), widths of long bones (WT1, WU, WH1) and negatively with distal part of tibia (LT2). It differenciates *A. peninsulae* from the other species arranged gradually along this axis from *A. flavicollis* (Central Europe) to *A. mystacinus* (Fig. 4, note: post hoc test revealed no significant difference between *A. peninsulae* vs *A. flavicollis* CE).

Phenetic comparisons of size-free data (see Appendix 2 for matrix of squared mahalanobis distances, and Fig. 5 for UPGMA tree) revealed clear distinctness of *A. (Apodemus) agrarius* (with basalmost position on phenetic tree), *A. (Apodemus) peninsulae*, *A. (Karstomys) mystacinus* and *A. (Sylvaemus) sylvaticus* (the subsequent branches) with respect to the group of remaining species/populations of the subgenus *Sylvaemus*. Within the latter group, *A. uralensis* and European *A. flavicollis* were most differentiated, while the samples from Near East populations of *A. hermonensis, A.hyrcanicus* and *A. flavicollis* clustered together.

We performed canonical analysis on size-free data in order to evaluate morphological relationships among studied samples (for this analysis the smallest sample,

ie *A. peninsulae,* was excluded). The positions of individual samples in a morphospace of the first three canonical roots are visualised in Fig. 6 and Fig. 7 (for loadings see Tab 2). *A. (Apodemus) agrarius* and *A. (Karstomys) mystacinus* were clearly separated by canonical axis 1, while the remaining samples belonging to the subgenera *Sylvaemus* formed more or less compact cluster in between. Canonical axis 2 segregated *A. agrarius* and *A. mystacinus* from the subgenus *Sylvaemus* within which *A. sylvaticus* formed the outlying cluster on the opposite side. Canonical axis 3 contributed to further differentiation of *Sylvaemus*. The species were arranged gradually from *A. uralensis* up to *A. flavicollis.*

Classification function resulting from DFA analyses of studied samples was then *a posteriori* applied to individuals of *A. peninsulae.* All individuals of *A. peninsulae* were assigned to *Sylvaemus* samples and not to *A. agrarius*, ie species representing the same subgenera (*Apodemus*). For visualisation of individuals of *A. peninsulae* in morphospace see Fig. 6 and Fig. 7.

Discussion

The mammalian postcranial skeleton consists of two distinct groups of segments – the limbs and the non-limb elements. Forelimb and hindlimb are serially homologous and share the subdivision on three segments (stylopod, zeugopod and autopod). Due to underlying regulation by *Hox* genes, their elements exhibit conservative covariance structure, which is similar even among only moderately related taxa as rodents and primates are (Young and Hallgrímsson 2005 and references herein). This fact may lead to correlated evolution of limb segments and reduced probability of their independent evolutionary change. On the other hand, locomotory performance and thus overall fitness of the animal is highly affected by changes in the relative proportion of limb segments. The observed differences between distantly and even between closely related taxa reported repeatedly in morphometric studies (see below) may, therefore, be likely interpreted as a result of an adaptive process (Young and Hallgrímsson 2005).

Non-limb elements of postcranial skeleton are putatively less causally integrated with limb elements (as concerned the regulatory genes), nevertheless, some of them still exhibit similar pattern of growth as particular limb elements, eg the case of axial skeleton

and femur (Melin *et al.* 2005). It conforms to the view that some elements of postcranial skeleton remain to be tied one to another, at least to some extent, either functionally or ontogenetically. Thus, it seems reasonable to evaluate postcranial measurements of all kinds (including associated body measurements) together.

There are differences in timing of growth among various elements of postcranial skeleton, eg the growth of the hind foot is completed much earlier than that of long bones, body and tail (Frynta and Žižková 1992, Melin *et al.* 2005). This phenomenon may further complicate the interpretation of correlations among studied traits. In our analyses, however, we avoided this potential problem by inclusion of fully grown individuals only.

Body size itself may play an important role in adaptive profile of the species, and sometimes undergoes an easy evolutionary change as clearly demonstrates the phenomenon of island gigantism reported repeatedly in *Apodemus* (Angerbjörn 1986, Libois and Fons 1990, Libois *et al.* 1993, Sarà and Casamento 1995). Therefore, it is not much surprising that vast majority of variation we found in postcranial skeleton measurements is explained by first principal component, and can be attributed to size differences. Nevertheless, in this paper we focus solely on the shape component of variance, ie on differences in relative size of particular bone segments, and the evolution of generalised body size will be elaborated elsewhere on the basis of both cranial and postcranial measurements.

Multivariate distances based on size adjusted data revealed that the main pattern of morphometric variation resembled that of phylogeny. Accordingly, the highest degree of morphological differentiation was found among the subgenera *Apodemus*, *Karstomys* and *Sylvaemus*. This fact, however, does not necessarily mean that adaptive ecological interpretation of these differences should be rejected (see Poe 2004). It is generally because of species that are related share their ecological strategies more likely, and thus the distribution of adaptive characters should follow the same phylogenetic pattern. In our case, the subgenus *Karstomys* contains only rock-dwelling species, but *A. agrarius* exhibits fairly exceptional ecological strategy within its subgenus. This fact encourages us to include *A. peninsulae*, the other representative of the subgenus *Apodemus* from East Asia exhibiting ecological requirements similar to those of some European *Sylvaemus* species, to our analyses. Interestingly enough, cluster analysis placed *A. peninsulae* outside the *Karstomys-Sylvaemus* cluster, but not together with *A. agrarius*. In the morphospace of the first two

canonical axes, *A. peninsulae* is placed close to the *Sylvaemus* species, but still in the direction towards *A. agrarius*. It seems to support the intuitive view that ecology of the species is somewhat associated with the shape of postcranial skeleton.

Fortunately, there is another procedure that may be used to verify the adaptive nature of observed morphological change, ie to evaluate agreement of our results with *a priori* hypotheses derived from functional interpretation of the characters as well as from empirical correlates between morphology and performance reported within other taxa. In this respect most studies were devoted to studying morphological adaptations confined to subterranean mode of life. These adaptations are mostly associated with digging activity of animals and comprise skeletal characters participating in strengthening of the forelimb skeleton (short and stout long bones) and in changes of size (enlarged medial epicondyl of humerus, deltoid process of humerus, teres major process of scapula) and position (increased ratio of in-lever arm to out-lever arm by eg distal position of deltoid process on humerus, prolongated olecranon on ulna) of areas for muscular attachments on bones (eg Heráň 1962a, Fernanándes *et al.* 2000, Warburton 1993). The similar but less prominent adaptation is reported also on hindlimb (short and robust long bones, eg Reed 1951, Warburton 1993), which participates in removing the scratched soil from burrow systems and accordingly in pelvis (long pelvis, Bohman 1939 ex Heráň 1962b) and vertebral column (long sacrum and its wide cranial part, short lumbal part eg Heráň 1962a, Schich 1971). Beside adaptations to digging there are also characters associated with movement in narrow burrow system (short tail, short ear, short limbs, eg Heráň 1961, Heráň 1962a, 1992, Böhme 1978). Unfortunately, there is only scarce information concerning adaptations tied up with other types of activities observed in *Apodemus* species. It includes adaptations on limb and vertebral column associated with arboreal activity (elongated limbs, loosen caput femoris, long lumbal part of vertebral column, broad cranial part of os sacrum, long tail, eg Dobroruka 1960, Heráň 1961, Heráň1962a, Schich 1971, Polk et. al. 2000) and fast terrestrial movement (long metatarsus, long lumbal part of vertebral column, caudal shift of acetabulum of pelvis, eg Heráň 1962b, Schich 1971).

After confronting the single characters responsible for observed morphological variation with ecological parameters of studied species we suppose following functional relationships. The first canonical root differentiates studied subgenera according to the

degree of their subterranean and digging activity. The *A. agrarius* possesses short ear and tail (LAU, LCD), short and robust tibia (LT1, LT2, WT1), broad pelvis (WP2) and broad ulna (WU), ie the characters likely associated with burrowing (ie partly subterranean and fossorial) mode of life of this species. But contrary to functional prediction, the *A. agrarius* has relatively long lumbal vertebra (VBL, but see later) and narrow collum femoralis (WF3). The opposite is true for *A. mystacinus*, the petricolous, non–burrowing species (Mirić 1964, Groll 1992), for which the long tail (with balance and support function), long tibia, and short lumbal vertebra (cf. Youlatos 1999) can be of high importance when moving in rocky environment (vertical jumping). The *Sylvaemus* species possess intermediate position along first canonical root in accordance with ecological predictions (they frequently use beside burrows also ground and above-ground nests), which differs from that of *A. agrarius* as well as *A. mystacinus*. They however form compact cluster in spite of supposed variation in degree of usage of subterranean space among individual species/populations.

Second axis placed *Sylvaemus* species (with extreme position of *A. sylvaticus*) to opposite position to *A. agrarius*. For such an arrangement of studied samples the characters associated with fast terrestrial movement and climbing on the one side and characters associated with subterranean and digging activity (ie range of characters, which could not be enforced along first canonical axis) on the other side are most likely responsible. So the burrowing and digging species - *A. agrarius*, which is bound to compact vegetation layer hindering fast movement, is characterised by short ear (LAU), short distal part of hindlimb (LT2, MET, LTP1), short forelimb (LH2, LU) with long olecranon (OLE) and long (LP2) and broad (WP1) pelvis. On the contrary long postacetabular part of pelvis (LP2) and long distal element on hindlimb (LT2, MET, LTP1) are likely convenient characters for fast running *Sylvaemus* species inhabiting open microhabitats or even for hopping movement on hindlimbs when travelling rapidly. The last mentioned mode of movement (hopping) was reported only in *A. sylvaticus* (Dieterlen 1965, Niethammer 1978) and can be responsible for separation of this species in morphospace along second canonical axis. Long distal elements of hindlimb and long forelimbs can be further linked with climbing activity, which was reported in *A. sylvaticus* and *A. flavicollis*.

The length of lumbal vertebra (VBL) and position of caput femoralis (WF3)

contribute most to the third canonical axis. It differentiates among *Sylvaemus* species, which are arranged successively in morphospace with *A. uralensis* (probably the least vertically active form of the subgenus Sylvaemus and *A. flavicollis* (frequently performing vertical activity – see under Introduction) being in extreme positions. This may be easily interpreted in adaptive manner: short lumbal vertebra found in *A. flavicollis* is possibly associated with vertical leaping (see Youlatos 1999 and references herein) and loosen caput femoralis with high degree of lateral movement of the hind limb, the character functionally associated with climbing.

In conclusion, morphometric examination of postcranial skeleton has revealed considerable variation among subgenera and to some extend also among particular species. Nevertheless, the observed differences are sometimes subtle and of deeply multivariate nature. Usually, interspecific differences follow functional predictions just in some of studied characters. Thus, our adaptive interpretations may sound too straightforward and simplified. Additional comparative data on performance of individual species are urgently required for proper understanding of morphology – ecology relationship.

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Table 1. PC loadings for 35 body and postcranial measurements. Analysis based on original log-transformed data. See Material and Methods for measurement abbreviations.

	LC	LCD	LTP1	LA	LT2	LT1	WT1	WT2	LF	WF1	WF2	LP2	LP1	WP1	WP2	LSF	WSF	SW1
PC1	-0,847	-0,853	-0,857	-0,709	-0,783	-0,918	-0,782	-0,886	-0,969	-0,896	-0,894	-0,937	-0,867	-0,866	-0,178	-0,797	-0,817	-0,895
PC2	-0,013	0,263	0,373	0,545	0,402	0,150	-0,131	-0,021	0,063	-0,076	-0,067	-0,182	-0,281	-0,289	0,066	-0,338	-0,203	-0,080
PC3	-0,016	-0,134	0,128	-0,095	-0,256	-0,010	0,321	0,220	-0,081	0,064	0,121	-0,041	-0,128	-0,157	0,789	-0,120	-0,078	-0,070

	SW2	VBW	VBL	WU	WH1	WH2	LS	WS1	WS2	LU1	LH2	OLE	LH1	WH3	WF4	WF3	MET
PC1	-0,859	-0,884	-0,744	-0,814	-0,864	-0,859	-0,945	-0,879	-0,889	-0,922	-0,873	-0,868	-0,902	-0,908	-0,700	-0,877	-0,745
PC2	-0,112	0,034	-0,416	-0,018	-0,096	-0,070	-0,091	-0,162	-0,160	0,266	0,256	-0,123	-0,096	0,010	-0,043	0,220	0,580
PC3	-0,180	-0,110	-0,139	0,312	0,269	0,046	-0,045	-0,035	-0,060	-0,093	-0,090	0,190	-0,011	0,107	-0,030	0,002	0,022

Table 2. Canonical variate loadings for 34 body and postcranial measurements. Analysis based on data adjusted by Mosimann method (size-free dat). See Material and Methods for measurement abbreviations.

	LC	LCD	LTP1	LA	LT2	LT1	WT1	WT2	LF	WF1	WF2	LP2	LP1	WP1	WP2	LSF	WSF
Root 1	0,209	-0,351	0,009	-0,186	-0,207	-0,168	0,210	0,064	-0,148	-0,061	-0,046	-0,077	0,155	-0,007	0,308	0,061	-0,099
Root 2	-0,077	-0,059	-0,266	-0,378	-0,270	-0,153	0,130	0,043	-0,110	0,125	0,142	0,226	0,160	0,169	-0,197	0,157	0,358
Root 3	-0,154	0,016	0,133	0,041	-0,042	-0,236	0,061	0,206	0,018	0,227	0,150	0,116	-0,047	-0,139	-0,064	-0,034	-0,082

	SW1	SW2	VBW	VBL	OLE	LU1	WU	LH1	LH2	WH1	WH2	LS	WS2	WH3	WF4	WF3	MET
Root 1	0,077	-0,045	-0,097	0,189	0,086	-0,031	0,178	-0,058	0,026	0,144	-0,152	0,106	0,107	-0,073	-0,002	-0,183	-0,054
Root 2	-0,105	0,033	-0,076	0,128	0,133	-0,299	-0,034	-0,011	-0,173	0,018	0,158	0,033	-0,014	0,028	0,128	-0,067	-0,505
Root 3	0,176	0,059	0,246	-0,380	0,047	-0,172	-0,124	-0,072	-0,043	-0,082	-0,120	-0,189	-0,271	-0,101	0,264	0,178	-0,181

Fig. 1. Postcranial measurements used in analyses. See Material and Methods for explanation of the measurement abbreviations.

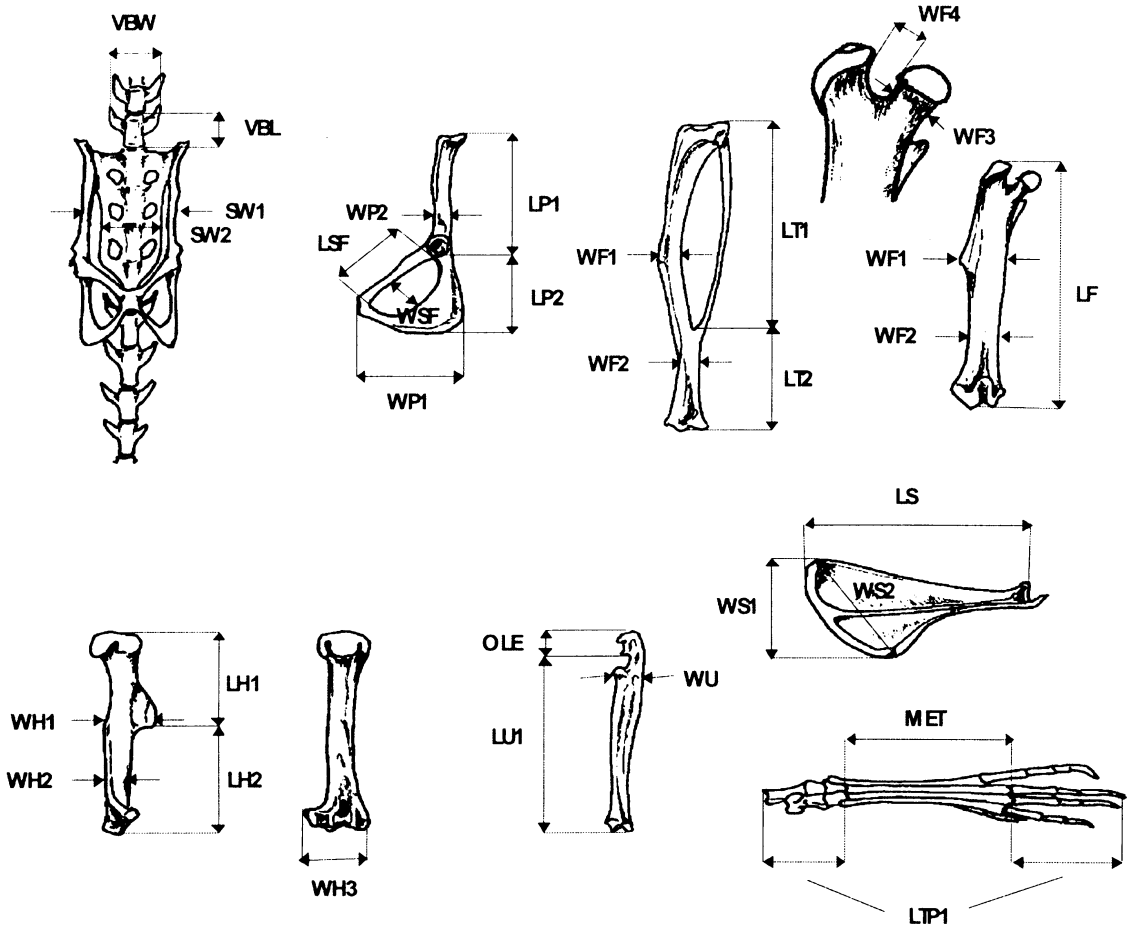

Fig. 2. Box plots of PC 1 scores derived from original log-transformed data

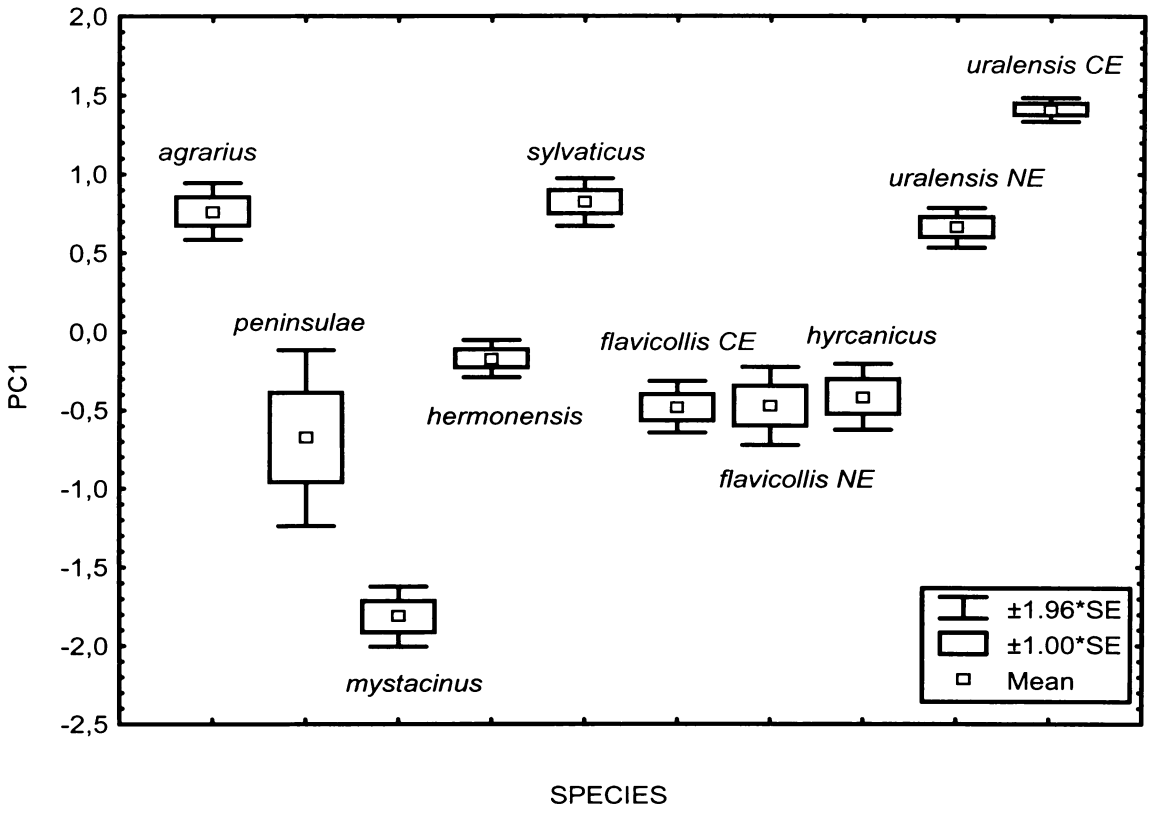

Fig. 3. Box plots of PC 2 scores derived from original log-transformed data

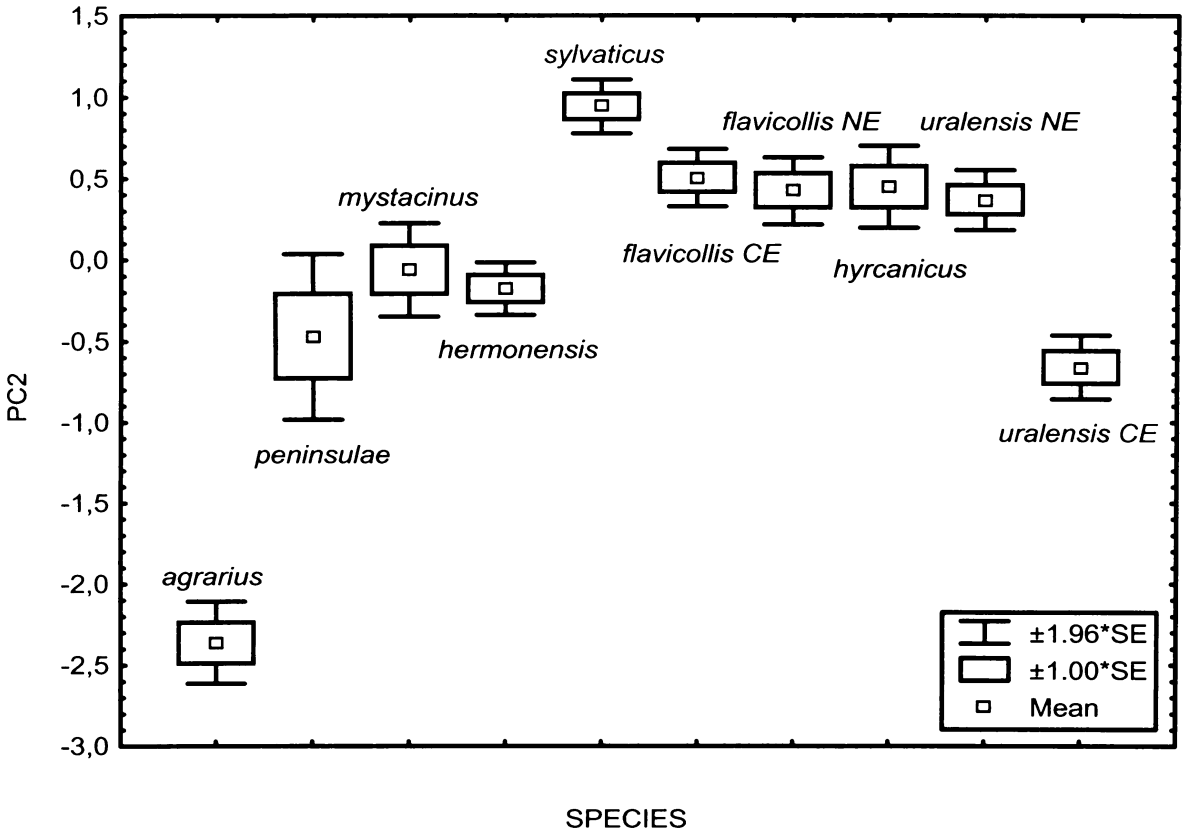

Fig. 4. Box plots of PC 3 scores derived from original log-transformed data

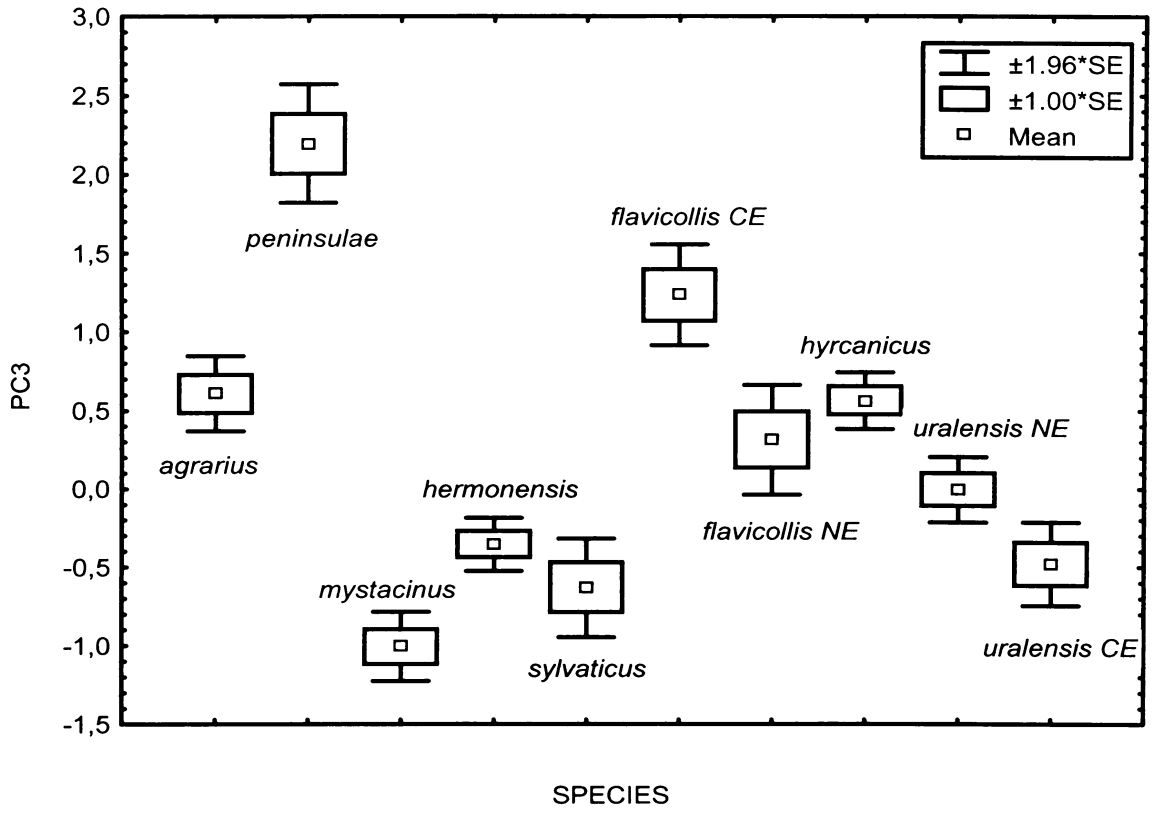

Fig. 5. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from data adjusted by Mosimann method (size-free data). CE - Central Europe, B – Balkans, NE – Near East.

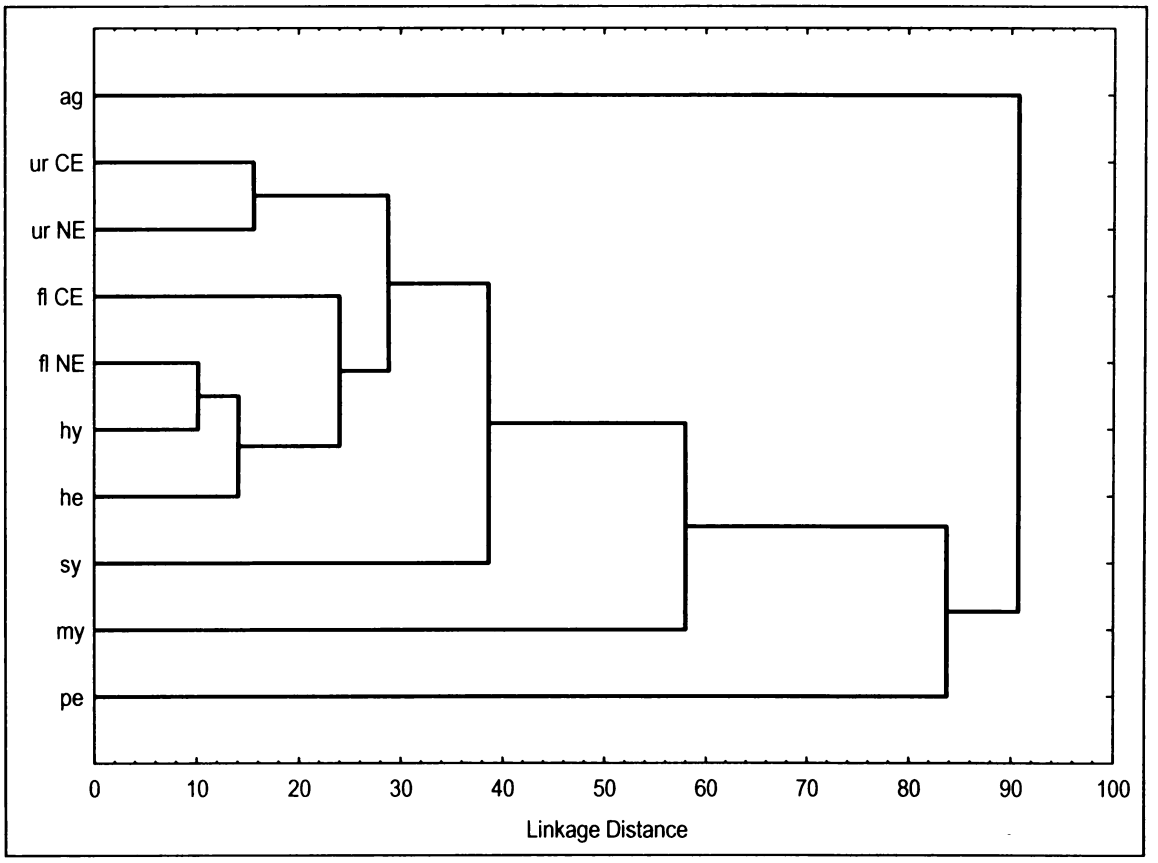

Fig. 6. Projection of 9 samples of *Apodemus* species onto the first two canonical variates as derived from data adjusted by Mosimann method (size-free data).

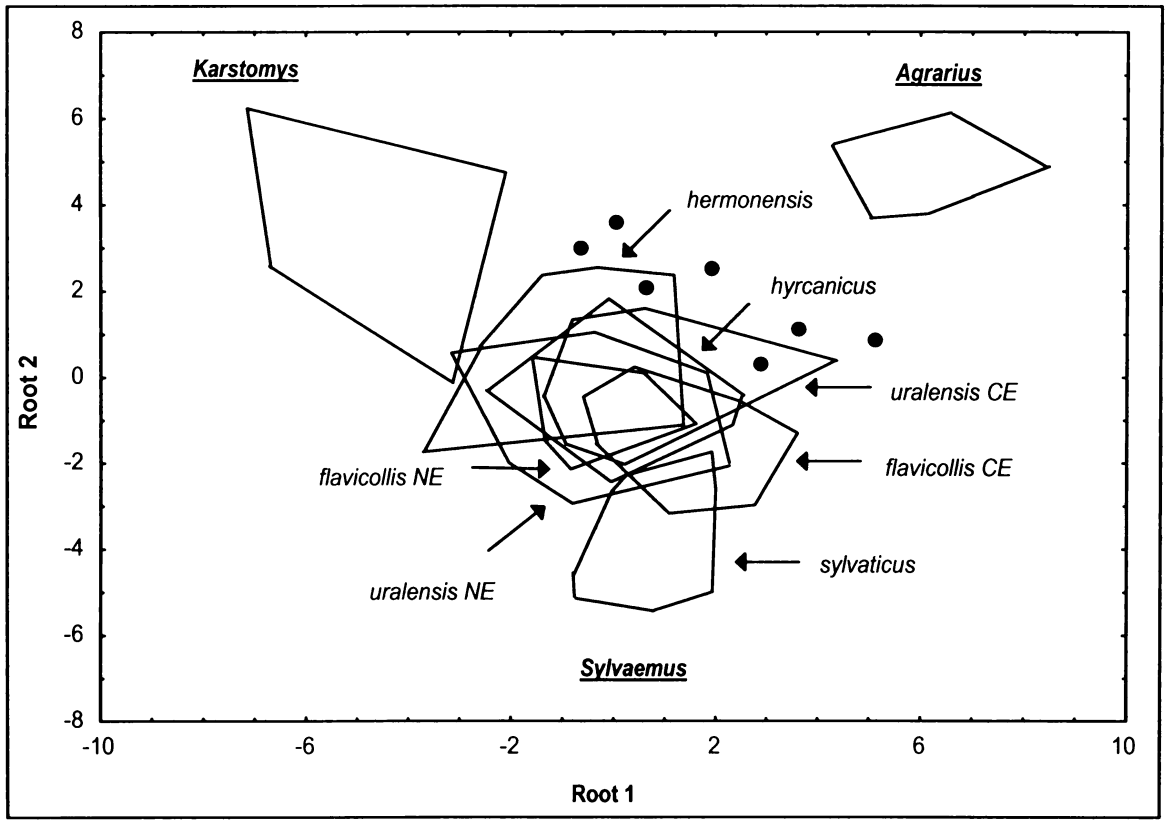

Fig. 7. Projection of 9 samples of *Apodemus* species onto the first and third canonical variates as derived from data adjusted by Mosimann method (size-free data).