

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

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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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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 al.* 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 murid 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. flavicollis* 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 generation 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, Yalnızcam Geçidi 5, Bağdaşan 3, Damar 8, Kabaca 8), Armenia (surroundings of Erevan 1) and Azerbaijan (Zakatally Reserve 1); Kirghyzstan – 29 specimens from Osh area.

Apodemus hermonensis: Near East – 52 specimens from eastern Turkey (Seyfe 1, Güzyurdu 4, Yalnızcam 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

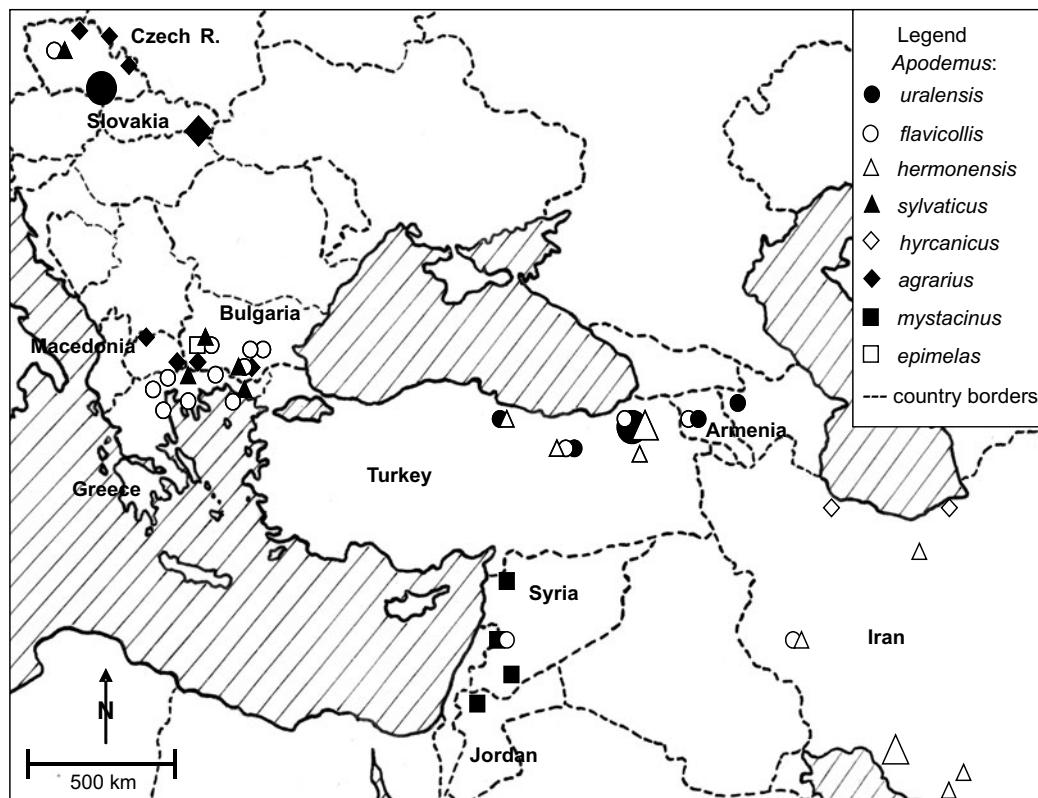


Fig. 1. Schematic map of the studied localities. Russian Far East (*A. peninsulae*) and Kirghyzstan (*A. uralensis*) are not depicted. Bigger sizes of symbols indicate more than one important localities where larger number of animals were collected.

– 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), RM¹L – first right upper molar length, RM¹W – first right upper molar width, RM³L – third right upper molar length, RM³W – third right upper molar width, RM₁L – first right lower molar length, RM₁W – 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

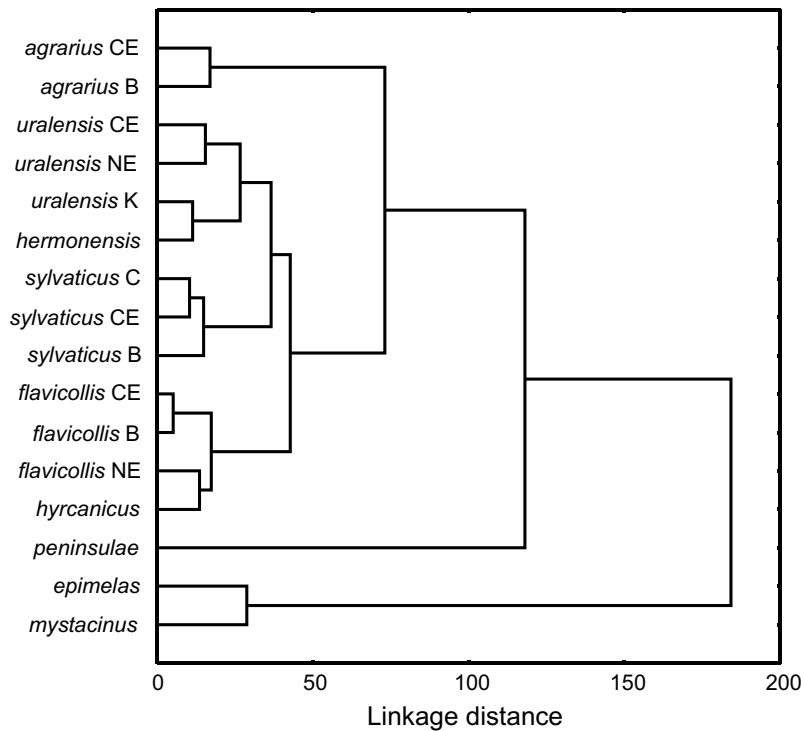


Fig. 2. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from original log-transformed data. Sixteen samples belonging to 3 subgenera were processed (*Apodemus*: *A. agrarius*, *A. peninsulae*; *Karstomys*: *A. epimelas*, *A. mystacinus*; *Sylvaemus*: *A. sylvaticus*,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

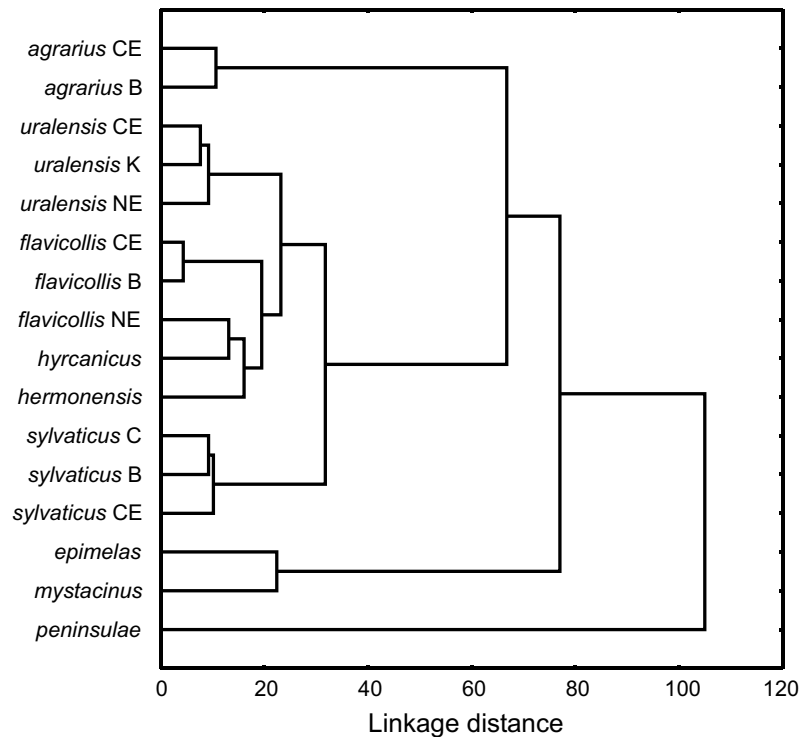


Fig. 3. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from size – adjusted data by using the Mosimann method. Sixteen samples belonging to 3 subgenera were processed (*Apodemus*: *A. agrarius*, *A. peninsulae*; *Karstomys*: *A. epimelas*, *A. mystacinus*; *Sylvaemus*: *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 Kirghyzstan.

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. syl-*

vaticus 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 Kirghyzstan in congruence with trees constructed from size-in data.

Subgenus *Sylvaemus*

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

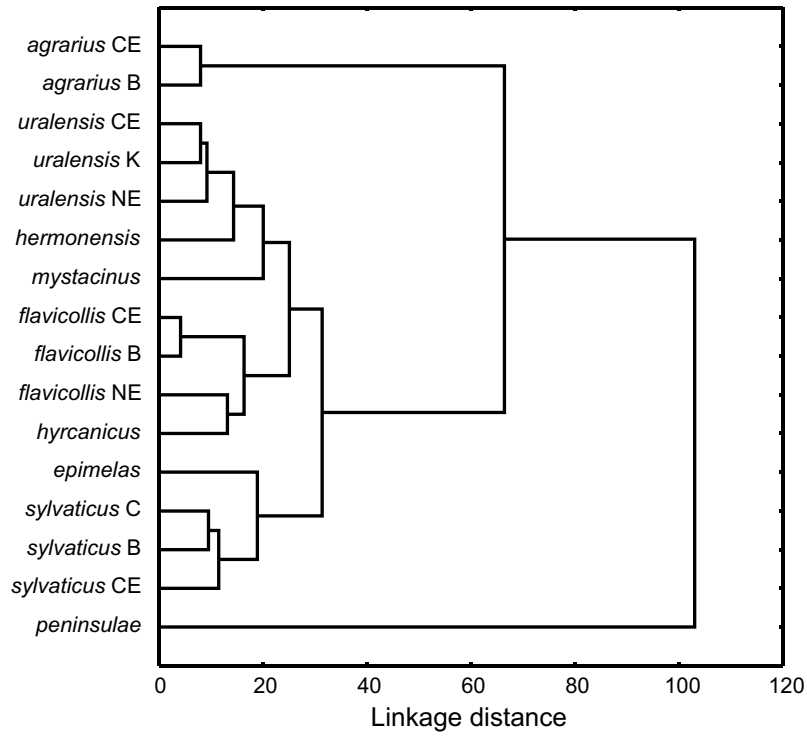


Fig. 4. Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from residuals on PC 1. Sixteen samples belonging to 3 subgenera were processed (*Apodemus*: *A. agrarius*, *A. peninsulae*; *Karstomys*: *A. epimelas*, *A. mystacinus*; *Sylvaemus*: *A. sylvaticus*, *A. flavicollis*,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

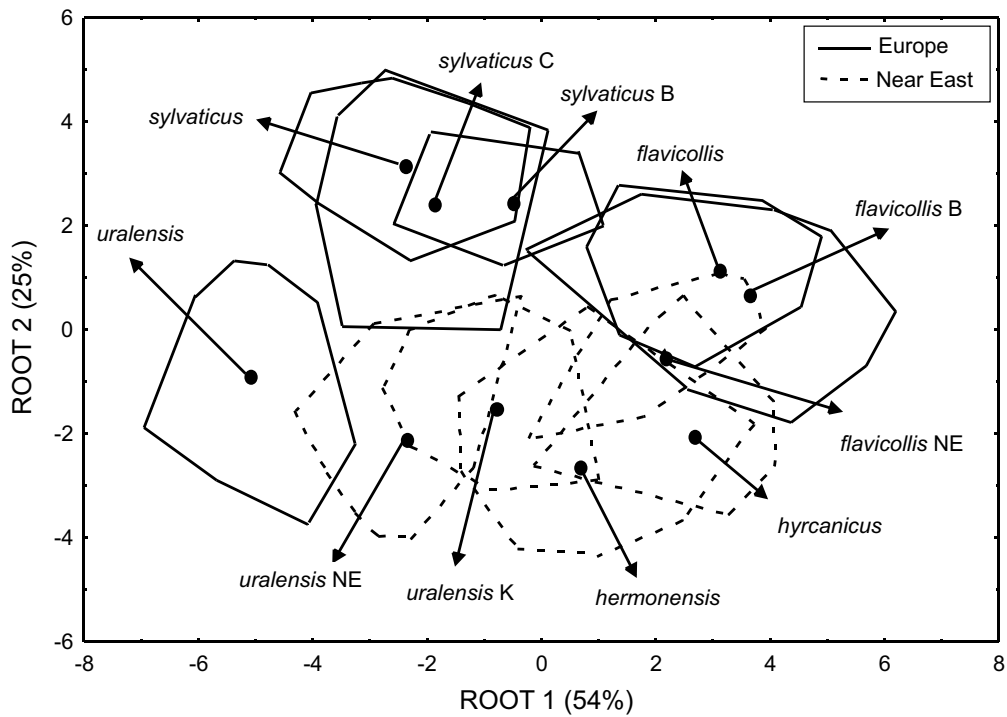


Fig. 5. Projection of 11 samples of five *Sylvaemus* species onto the first two canonical variates as derived from original log-transformed measurements. K – Kirghyzstan, C – laboratory colony, B – Balkans, NE – Near East. Solid circles depict sample means.

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 ¹ W	0.439	0.154
RM ¹ L	0.565	0.153
RM ³ W	0.396	-0.001
RM ³ L	0.413	-0.071
PAL	0.535	-0.398
RM ₁ L	0.504	0.152
MZ	0.215	-0.183
RM ₁ W	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.

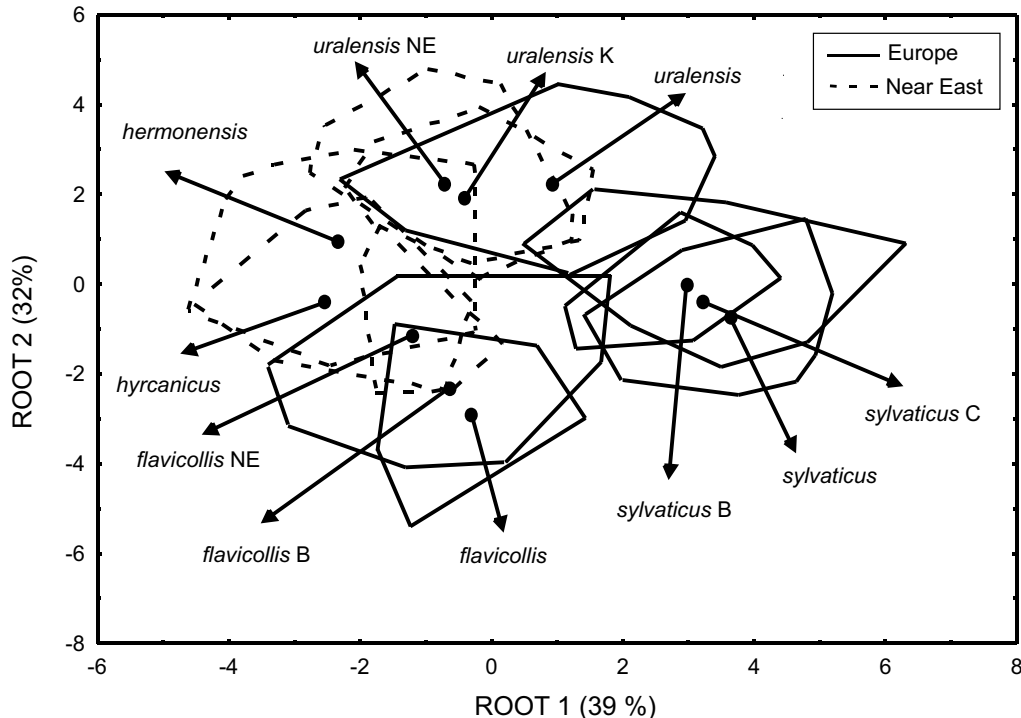


Fig. 6. Projection of 11 samples of five *Sylvaemus* species onto the first two canonical variates as derived from size-adjusted data by using the Mosimann method. K – Kirghyzstan, C – laboratory colony, B – Balkans, NE – Near East. Solid circles depict sample means.

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 ¹ W	0.298	0.022
RM ¹ L	0.119	-0.275
RM ³ W	-0.040	-0.143
RM ³ L	-0.123	-0.115
PAL	-0.478	-0.014
RM ₁ L	0.167	-0.193
MZ	-0.193	0.009
RM ₁ W	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 ¹ W	-0.232	-0.098
RM ¹ L	-0.227	0.061
RM ³ W	-0.028	0.071
RM ³ L	0.048	0.016
PAL	0.427	0.116
RM ₁ L	-0.235	-0.074
MZ	0.142	-0.132
RM ₁ W	-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

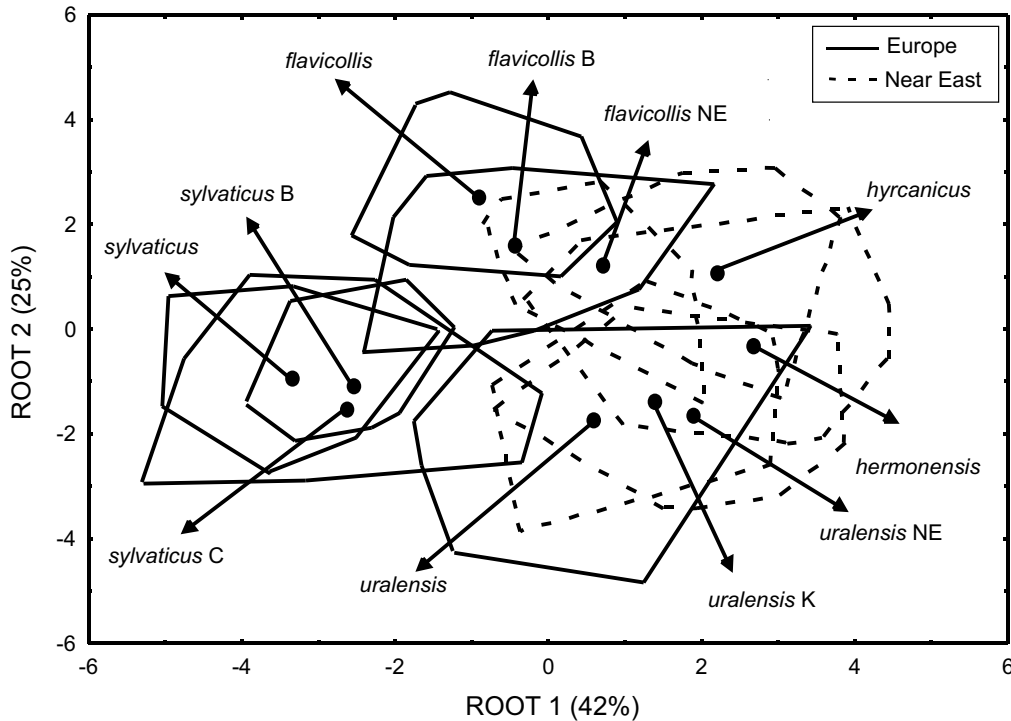


Fig. 7. Projection of 11 samples of five *Sylvaemus* species onto the first two canonical variates as derived from residuals on PC 1. K – Kirghyzstan, C – laboratory colony, B – Balkans, NE – Near East. Solid circles depict sample means.

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 (Mezhzhherin 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. fla-*

vicollis (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 attributed to phylogeny itself because, neither European nor Near East assemblage 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 further 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 murid 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 Palaearctics 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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References

- Bellinva E. 2004. A phylogenetic study of the genus *Apodemus* by sequencing the mitochondrial DNA control region. *Journal of Zoological Systematics and Evolutionary Research* 42: 289–297.
- Bellinva E., Munclinger P. and Flegr J. 1999. Application of the RAPD technique for a study of the phylogenetic relationships among eight species of the genus *Apodemus*. *Folia Zoologica* 46: 193–199.
- Böhme W. 1978. *Apodemus agrarius* (Pallas, 1771) – Brandmaus. [In: *Handbuch der Säugetiere Europas, Band I., Nagetiere* 1. J. Niethammer and F. Krapp, eds]. Akademische Verlagsgesellschaft, Wiesbaden: 368 – 381.
- Burnaby T. P. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics* 22: 96–110.
- Chelomina G. N., Suzuki H., Tsuchiya K., Moriwaki K., Lyapunova E. A. and Voronstov N. N. 1998. Sequencing of the mt DNA cytochrome b gene and reconstruction of the maternal relationships of wood and field mice of the genus *Apodemus* (Muridae, Rodentia). *Genetika* 34: 650–661. [In Russian with English summary]
- Čiháková J., Exnerová A., Sádlo J. and Frynta D. 1993. Many-sided evaluation of the extensive synchronous sampling of small mammals (Insectivora, Rodentia) in lowland forest. *Acta Societatis Zoologicae Bohemicae* 57: 1 – 16.
- Filippucci M. G. 1992. Allozyme variation and divergence among European, Middle Eastern, and North African species of the genus *Apodemus* (Rodentia, Muridae). *Israel Journal of Zoology* 38: 193–218.
- Filippucci M. G., Cristaldi M., Tizi L. and Contoli L. 1984. [Morphological and morphometric data, about *Apodemus (Sylvaemus)* population of central and southern Italy tested by electrophoresis]. *Supplemento alle Ricerche di Biologia della Selvaggina* 9, Bologna: 85–126. [In Italian]
- Filippucci M. G., Macholán M. and Michaux J. R. 2002. Genetic variation and evolution in the genus *Apodemus* (Muridae, Rodentia). *Biological Journal of Linnean Society* 75: 395–419.
- Filippucci M. G., Simson S. and Nevo E. 1989. Evolutionary biology of the genus *Apodemus* Kaup, 1829 in Israel. Allozymic and biometric analyses with description of a new species: *Apodemus hermonensis* (Rodentia: Muridae). *Bollettino di Zoologia* 56: 361–376.
- Filippucci M. G., Storch G. and Macholán M. 1996. Taxonomy of the genus *Sylvaemus* in western Anatolia – morphological and electrophoretic evidence. *Senckenbergiana Biologica* 75: 1–14.
- Frynta D., Mikulová P., Suchomelová E. and Sádlová J. 2001. Discriminant analysis of morphometric characters in four species of *Apodemus* (Muridae: Rodentia) from Eastern Turkey and Iran. *Israel Journal of Zoology* 47: 243–258.
- Frynta D., Vohralík V., Řezníček J. 1994. Small mammals (Insectivora, Rodentia) in the city of Prague: distributional patterns. *Acta Societatis Zoologicae Bohemicae* 58: 151 – 176.
- Frynta D. and Žížková M. 1992. Postnatal growth of Wood mouse (*Apodemus sylvaticus*) in captivity. [In: *Prague Studies in Mammalogy*. I. Horáček and V. Vohralík, eds]. Charles University Press, Prague: 57–69.
- Garland T. 1994. Phylogenetic analyses of lizard endurance capacity in the relation to body size and body temperature. [In: *Lizard ecology, Historical and Experimental perspectives*. L. J. Vitt and E. R. Pianka, eds]. Princeton University Press, Princeton, New Jersey: 237–259.
- Hille A., Tarkhnishvili D., Meinig H. and Hutterer R. 2002. Morphometrics, biochemical and molecular traits in Caucasian wood mice (*Apodemus/Sylvaemus*), with remarks on species divergence. *Acta Theriologica* 47: 389–416.
- Janžekovic F. and Kryštufek B. 2004. Geometric morphometry of the upper molars in European wood mice *Apodemus*. *Folia Zoologica* 53: 47–55.
- Kratochvíl J. 1962. Notiz zur Ergänzung der Verbreitung von *Apodemus agrarius* und *A. microps* in der Tschechoslowakei. *Zoologické Listy* 11: 15–25. [In Czech with German summary]
- Kryštufek B. 2002. Identity of four *Apodemus (Sylvaemus)* types from the eastern Mediterranean and the Middle East. *Mammalia* 66: 43–51.
- Kryštufek B. and Stojanovski L. 1996. *Apodemus sylvaticus stankovici* is a synonym of *Apodemus flavicollis*. *Folia Zoologica* 45: 1–7.
- Lavrenchenko L. A. and Likhnova O. P. 1995. Allozymic and morphological variability in 3 syntopic species of wood mice from the subgenus *Sylvaemus* (Rodentia, Muridae, *Apodemus*) from Daghestan. *Zoologicheskii*

- Zhurnal 74: 107–119. [In Russian with English summary]
- Macholán M. 2001. Multivariate analysis of morphometric variation in Asian *Mus* and Sub-Saharan *Nannomys* (Rodentia: Muridae). *Zoologischer Anzeiger* 240: 7–14.
- Macholán M., Filippucci M. G., Benda P., Frynta D. and Sádlová J. 2001. Allozyme variation and systematics of the genus *Apodemus* (Muridae: Rodentia) in Asia Minor and Iran. *Journal of Mammalogy* 82: 799–813.
- Marsh A. C. W. and Harris S. 2000. Partitioning of woodland resources by two sympatric species of *Apodemus*: lessons for the conservation of yellow-necked mouse (*A. flavicollis*) in Britain. *Biological Conservation* 92: 275–283.
- Martin Y., Gerlach G., Schlotterer C. and Meyer A. 2000. Molecular phylogeny of European murid rodents based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution* 16: 37–47.
- Mezhzherin S. V. 1990. Allozyme variability and genetic divergence of Long-tailed mice of subgenus *Sylvaemus* (Ognev et Vorobiev). *Genetika* 26: 1046–1054. [In Russian with English summary]
- Mezhzherin S. V. 1991. On specific distinctness of *Apodemus* (*Sylvaemus*) *ponticus* (Rodentia, Muridae). *Vestnik Zoologii, Kiev* 1991 (6): 34–40. [In Russian with English summary]
- Mezhzherin S. V. 1997a. Revision of mice genus *Apodemus* (Rodentia, Muridae) of Northern Eurasia. *Vestnik Zoologii, Kiev* 31 (4): 29–41. [In Russian with English summary]
- Mezhzherin S. V. 1997b. Genetic differentiation and phylogenetic relationships among Palaearctic mice (Rodentia, Muridae). *Genetika* 33: 78–86. [In Russian with English summary]
- Mezhzherin S. V., Zykov A. E. 1991. Genetic divergence and allozyme variation in mice of the genus *Apodemus* s. lato (Muridae: Rodentia). *Citologiya i Genetika* 25 (4): 51–59. [In Russian with English summary]
- Michaux J., Bellinva E. and Lymberakis P. 2005. Taxonomy, evolutionary history and biogeography of the Broad-toothed Field Mouse (*Apodemus mystacinus*) in the Eastern Mediterranean area based on mitochondrial and nuclear genes. *Biological Journal of the Linnean Society* 85: 53–64.
- Michaux J. R., Chevret P., Filippucci M. G. and Macholán M. 2002. Phylogeny of the genus *Apodemus* with a special emphasis to the subgenus *Sylvaemus* using the nuclear IRBP gene and two mitochondrial markers: cytochrome b and 12s rRNA. *Molecular Phylogenetics and Evolution* 23: 123–136.
- Michaux J. R., Libois R. and Filippucci M. G. 2005. So close and so different: comparative phylogeography of two small mammal species, the Yellow-necked fieldmouse (*Apodemus flavicollis*) and the Woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. *Heredity* 94: 52–63.
- Michaux J. R., Libois R., Paradis E. and Filippucci M. G. 2004. Phylogeographic history of the yellow-necked field mouse (*Apodemus flavicollis*) in Europe and in the Near and Middle East. *Molecular Phylogenetics and Evolution* 32: 788–798.
- Michaux J. R., Magnanou E., Paradis E., Nieberding C. and Libois R. 2003. Mitochondrial phylogeography of the woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. *Molecular Ecology* 12: 685–697.
- Mikulová P. and Frynta D. 2001. Test of character displacement in urban populations of *Apodemus sylvaticus*. *Canadian Journal of Zoology* 79: 794–801.
- Mitchell-Jones A. J., Amori G., Bogdanowicz W., Kryštufek B., Reijnders P. J. H., Spitzenberger F., Stubbe M., Thissen J. B. M., Vohralík V. and Zima J. 1999. The atlas of European mammals. Academic Press, London: 1–484.
- Montgomery W. I. 1978. Studies on the distributions of *Apodemus sylvaticus* (L.) and *A. flavicollis* (Melchior) in Britain. *Mammal Review* 8: 177–184.
- Musser G. G., Brothers E. M., Carleton M. D. and Hutterer R. 1996. Taxonomy and distributional records of Oriental and European *Apodemus*, with a review of the *Apodemus-Sylvaemus* problem. *Bonner Zoologische Beiträge* 46: 143–190.
- Mosimann J. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association* 65: 930–945.
- Obrtel R. and Holišová V. 1983. Winter and spring diets of three coexisting *Apodemus* spp. *Folia Zoologica* 32: 291–302.
- Özkan B. and Kryštufek B. 1999. Wood mice, *Apodemus* of two Turkish islands: Gökceada and Bozcaada. *Folia Zoologica* 48: 17–24.
- Panzironi C., Cerone G., Cristaldi M. and Amori G. 1994. A method for the morphometric identification of southern Italian populations of *Apodemus* (*Sylvaemus*). *Hystrix, n.s.*, 5: 1–16.
- Popov V. 1993. Discriminant criteria and comparative study on morphology and habitat selection of *Apodemus sylvaticus* (Linnaeus, 1758) and *Apodemus flavicollis* (Melchior, 1834) (Mammalia, Rodentia, Muridae) in Bulgaria. *Acta Zoologica Bulgarica* 46: 100–111.
- Reutter B. A., Hausser J. and Vogel P. 1999. Discriminant analysis of skull morphometric characters in *Apodemus sylvaticus*, *A. flavicollis*, and *A. alpicola* (Mammalia; Rodentia) from the Alps. *Acta Theriologica* 44: 299–308.
- Reutter B. A., Petit E., Brünner H., Vogel P. 2003. Cytochrome b haplotype divergences in West European *Apodemus*. *Mammalian Biology* 68: 153–164.
- Serizawa K., Suzuki H. and Tsuchia K. 2000. A phylogenetic view on species radiation in *Apodemus* inferred from variation of nuclear and mitochondrial genes. *Biochemical Genetics* 38: 27–40.
- Spitzenberger F., Steiner H. M. 1967. Die Ökologie der Insectivora und Rodentia (Mammalia) der Stockerauer Donau – Auen von Stockerau (Niederösterreich). *Bonner Zoologische Beiträge* 18: 258–296.
- Stanko M. 1994. Small mammal communities of windbreaks and adjacent fields in the Eastern Slovakian Lowlands. *Folia Zoologica* 43: 135–143.

- Steiner H. M. 1968. Untersuchungen über die Variabilität und Bionomie der Gattung *Apodemus* (Muridae, Mammalia) der Donau-Auen von Stockerau (Niederösterreich). *Zeitschrift für Wissenschaftliche Zoologie* 177: 1–96.
- Suzuki H., Sato J. J., Tsuchiya K., Luo J., Zhang Y. P., Wang Y. X. and Jiang X. L. 2003. Molecular phylogeny of wood mice (*Apodemus*, Muridae) in East Asia. *Biological Journal of Linnean Society* 80: 469–481.
- Tvrtrković N. 1979. Identification of sibling species from subgenus *Sylvaemus* Ognev & Vorobiev 1923 (Rodentia: Mammalia). *RAD Jugoslavenske akademije znanosti i umjetnosti, Razred za prirodne znanosti* 18: 155–186. [In Croatian with German summary]
- Vogel P., Maddalena T., Mabile A. and Paquet G. 1992. Confirmation biochimique du statut spécifique du mulot alpestre *Apodemus alpicola* Heinrich, 1952 (Mammalia, Rodentia). *Bulletin de la Societe' Vaudoise des Sciences Naturelles* 80: 471–481.
- Vohralík V. 1985. Notes on the distribution and the biology of small mammals in Bulgaria (Insectivora, Rodentia). I. *Acta Universitatis Carolinae – Biologica* 1981: 445–461.
- Vohralík V., Frynta D., Mikulová P., Benda P. and Nová P. 2002. Multivariate morphometrics of *Apodemus mystacinus* in the Near East and its divergence from European *A. m. epimelas* (Mammalia: Rodentia). *Israel Journal of Zoology* 48: 135–148.
- Vohralík V. and Sofianidou T. S. 1987. Small mammals (Insectivora, Rodentia) of Macedonia, Greece. *Acta Universitatis Carolinae – Biologica* 1985: 319–354.
- Vohralík V. and Sofianidou T. S. 1992a. Small mammals (Insectivora, Rodentia) of Thrace, Greece. *Acta Universitatis Carolinae – Biologica* 36: 341–369.
- Vohralík V. and Sofianidou T. S. 1992b. New records of *Apodemus agrarius* (Mammalia: Rodentia) in Greece and the distribution of the species in the south of the Balkans. [In: *Prague Studies in Mammalogy*. I. Horáček and V. Vohralík, eds]. Charles University Press, Prague: 217–220.
- Vorontsov N. N., Boyeskorov G. G., Mezhzherin S. V., Lypunova E. A. and Kandaurov A. E. 1992. Systematics of the Caucasian wood mice of the subgenus *Sylvaemus* (Mammalia: Rodentia, *Apodemus*). *Zoologicheskii Zhurnal* 71: 119–131. [In Russian with English summary]
- West-Eberhard M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* 20: 249–278.
- West-Eberhard M. J. 2003. *Developmental Plasticity and Evolution*. Oxford University Press, Oxford: 1–794.
- Zejda J. 1965. Habitat of the Long-tailed Field Mouse (*Apodemus sylvaticus*) in the Lowland Region. *Zoologické Listy* 14: 301 – 316. [In Czech with English summary]

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