

Interspecific morphometric variation in the postcranial skeleton in the genus *Apodemus*

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ABSTRACT. Wood mice (genus *Apodemus*) are common murid rodents in the Palearctic region. In spite of the fact that they exhibit high phenotypic similarity, individual species (populations) differ in their preferred habitat (woodlands, steppes-fields, rocks) and behaviour (tendency to digging, jumping, climbing). It is therefore of special interest to evaluate interspecific (inter-population) variability in postcranial skeleton within this group and to suggest ecological interpretations of observed differences. We studied skeletons of 265 wood mice belonging to seven species from Europe and the Middle East: *Apodemus agrarius* (subgenus *Apodemus*), *A. mystacinus* (subgenus *Karstomys*), *A. hyrcanicus*, *A. witherbyi*, *A. uralensis* (= *microps*), *A. flavicollis* and *A. sylvaticus* (subgenus *Sylvaemus*). Thirty five postcranial and body measurements were obtained and analysed using multivariate statistics. The multivariate analysis, based on size adjusted data, revealed clear morphological separation among species belonging to different subgenera. The morphological characters responsible for this separation and the position of the control sample of *A. peninsulae* (belongs to the same subgenus as *A. agrarius*, but differs in preferred habitat) in morphospace support the view, that ecology participated in the shaping of the postcranial skeleton of the studied species. *A. agrarius* possesses the characters associated with digging activity, *A. mystacinus* with jumping and *Sylvaemus* species with fast terrestrial movement and climbing. However, there were found only subtle morphological differences among individual *Sylvaemus* species, in spite of variability in their ecological requirements.

KEY WORDS : morphometrics, ecomorphology, wood mice, *Sylvaemus*, *Apodemus*, *Karstomys*

INTRODUCTION

Muroid rodents (family Muridae) represent a highly diversified mammalian clade inhabiting nearly all habitat types. Consequently, individual rodent species exhibit a suite of characteristics that are associated with a particular lifestyle. These may comprise behaviour (adaptive profile: DEWSBURY et al., 1982), locomotor performance (*sensu* GARLAND, 1994) and morphology (e.g. PRICE, 1993). Closely related rodent taxa exhibiting different ecological and behavioural strategies, such as wood mice of the genus *Apodemus* Kaup, 1829, may serve as an appropriate model for understanding the evolution of species-specific design.

Wood mice are common murid rodents in the Palearctic 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 *Apodemus* species are opportunistic seed eaters that also consume insects and diverse additional vegetable components (e.g. MIRIĆ, 1966; HOLIŠOVÁ, 1967; HOLIŠOVÁ & OBRTEL, 1977; 1980; BABINSKA-WERKA, 1981; OBRTEL & HOLIŠOVÁ, 1983; GEBZYNSKA et al., 1987; MONTGOMERY & MONTGOMERY, 1990; HEROLDVÁ, 1994; ROGERS & GORMAN, 1995). They share generalized muroid morphology and exhibit high phenotypic similarity among species (e.g. FRYNTA et al., 2006), but 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 e.g. MARTIN et al., 2000; MICHAX et al., 2002; BELLINIA, 2004) corresponding to traditionally recognized subgenera: *Apodemus*, *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 Palearctics. It has only recently (early Holocene) extended its range from the Far East westwards to Europe (BÖHME, 1978). *A. agrarius* is predominantly field-dwelling and associated with crop-fields, grasslands, and open wet habitats, especially along rivers and streams (KRATOCHVÍL, 1962; 1977; ZEJDA, 1967; KARASEVA et al., 1992).

The subgenus *Karstomys* consists of only two species: *A. epimelas* (Nehring, 1902) from the Balkans and *A. mystacinus* (Danford and Alston, 1877) from the Island of Crete and the Middle East (see VOHRALÍK et al., 2002). Both of these species are specialised rock-dwellers and represent the largest forms of the genus *Apodemus*. They do not make their own burrows like other studied *Apodemus* species, instead using rock cavities as nests (MIRIĆ, 1966; GROLL, 1992).

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 Central Europe, they exhibit contrasting ecological strategies. *A. flavicollis* is

a forest-dweller (e.g. STEINER, 1968; MONTGOMERY, 1977; MARSH & HARRIS, 2000), *A. uralensis* a field-dweller (e.g. 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 (e.g. ZEJDA, 1965; STEINER, 1968; ČIHÁKOVÁ et al., 1993; FRYNTA et al., 1994). These preferences were clearly supported by a study of rodent assemblages in windbreaks and adjacent fields performed in southern Moravia (Central Europe; PELIKÁN, 1986). Moreover, *A. flavicollis* and *A. sylvaticus* are known to exhibit considerable arboreal activity (*A. flavicollis*: BOROWSKI, 1962; HOLIŠOVÁ, 1969; MONTGOMERY, 1980; JUŠKAITIS, 1995; *A. sylvaticus*: MONTGOMERY, 1980; SANTOS & TELLERÍA, 1991; TATTERSALL & WHITBREAD, 1994 and references therein). Both species are able to use tree cavities instead of subterranean nests.

While the habitat requirements of European species have been studied in detail (see above), only fragmentary information is available for the *Sylvaemus* species of the Middle 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. witherbyi* (Thomas, 1902), may be found syntopically. Nevertheless, *A. witherbyi* 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).

The different habitat preferences described above may be associated with different locomotor performance of particular *Apodemus* species and possibly adaptive evolution of relevant morphological traits. We can assume that species living in open microhabitats (including forest/shrub habitats without dense undercover) should possess morphological traits associated with fast running and jumping. Species inhabiting forest habitats should possess morphological traits associated with climbing. Species using subterranean nests should possess morphological traits associated with digging.

Unfortunately, there is only limited information concerning the locomotor performance and morphology of individual *Apodemus* species. When subjected to ten minute laboratory tests for exploratory behaviour (FRYNTA, 1992; 1994), the *Apodemus* fall 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 the European population of *A. agrarius*, had the lowest activity. The species of the subgenus *Sylvaemus* have a fairly intermediate position. Jumping was correlated with activity scores (FRYNTA, 1994). This behaviour has never been recorded in a European population of *A. agrarius* during the experiments. It was rare in *A. uralensis* (mean=0.4 jumps per 10min test),

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 (e.g. FILIPPUCCI et al., 1984; POPOV, 1993; PANZIRONI et al., 1994; LAVRENCHENKO & LIKHOVA, 1995; ÖZKAN & KRYŠTUFEK, 1999; REUTTER 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 have analysed multivariate cranial morphometry of nine *Apodemus* species (16 samples, FRYNTA et al., 2006) and found a good correspondence between our phenetic tree and the current phylogenetic hypothesis based on DNA sequences (MICHAX et al., 2002; BELLINIA, 2004).

In contrast, limited information is available about the morphological traits of *Apodemus* species that may be associated with their type of locomotion. Attention to date has focused on some external measurements. The lengths of the tail and the hind-foot and the eye diameter have traditionally been considered by field workers to distinguish among the European *Sylvaemus* species of similar appearance, whereas the small eye diameter and the short tail and hind-foot in *A. uralensis* (as well as in *A. agrarius* of the subgenus *Apodemus*) are supposed to be attributed to the high proportion of activity in burrows in this species (HOLIŠOVÁ et al., 1962; NIETHAMMER & KRAPP, 1978). Similarly, the length of vibrissae is expected to be functionally related to the diameter of investigated space. The subterranean species usually have 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*.

To be able to explain the interspecific variation in morphology found within *Apodemus*, we need to make use of the functional interpretation of the characters and the relationship between morphology and locomotor performance reported within other taxa. In this respect most studies are devoted to studying morphological adaptations for a subterranean mode of life. These adaptations are mostly associated with digging activity of animals and comprise skeletal characters participating in: 1) strengthening of the forelimb skeleton (short and stout bones), 2) changes of size of areas for muscular attachments on bones (e.g. enlarged medial and lateral epicondyle of humerus, deltoid process of humerus, teres major process and acromion process of scapula) and 3) changes of position (increased ratio of in-lever arm to out-lever arm by e.g. distal position of deltoid process on humerus, elongated olecranon on ulna) of areas for muscular attachments on bones (e.g. HERÁŇ, 1962a; HILDEBRAND, 1985; NEVO, 1999; FERNÁNDES et al., 2000; STEIN, 2000; ELISSAMBURU & VIZCAÍNO, 2004; LAGARIA & YOULATOS, 2006; SAMUELS & VAN VALKENBURGH, 2008; unpublished data¹). Similar but

¹ WARBURTON NM (1993). Functional morphology and evolution of marsupial moles (Marsupialia, Notoryctemorphia). MSc. thesis. The University of Western Australia, Perth: 1-237.

less prominent modifications are reported also for the hind limbs (short and robust long bones, enlarged epicondyle of femur, elongated tibial tuberosity, short tarsal and metatarsal bones, e.g. REED, 1951; STEIN, 2000; ELISSAMBURU & VIZCAÍNO, 2004; SAMUELS & VAN VALKENBURGH, 2008; unpublished data¹), pelvis and axial skeleton (reduced pelvis fused to the sacrum, acetabulum shifted to the spinal axis, long ischium with massive ischial tuberosity, massive wings of ilium, elongated sacrum with its widened cranial part, short lumbar part of spinal axis e.g. HERÁŇ, 1962a; 1962b; SCHICH, 1971; NEVO, 1999; STEIN, 2000), which participate in soil removal from burrow systems and bracing the body against tunnel walls. Besides adaptations to digging there are also characters associated with movement in a narrow burrow system (short tail, short ears, short limbs, e.g. HERÁŇ, 1961; HERÁŇ, 1962a, 1992; BÖHME, 1978; NEVO, 1999; STEIN, 2000). Unfortunately, there is little information concerning adaptations associated with other types of activities observed in *Apodemus* species. It includes adaptations on limbs and vertebral column associated with arboreal activity (elongated and gracile limbs, short olecranon on ulna, loose femoral head, long lumbar part of vertebral column, broad cranial part of sacrum, long tail, e.g. DOBRORUKA, 1960; HERÁŇ, 1961; HERÁŇ, 1962a; SCHICH, 1971; POLK et al., 2000; SAMUELS & VAN VALKENBURGH, 2008) and fast terrestrial movement (short distal extension of greater trochanter of femur, long metatarsal bones, long lumbar part of vertebral column, caudal shift of acetabulum of pelvis, e.g. HERÁŇ, 1962b; SCHICH, 1971; ELISSAMBURU & VIZCAÍNO, 2004). There are also studies that deal with inner construction of bones as e.g. the amount and distribution of cortical bone in respect to ecology of studied species (BIKNEVICIUS, 1993).

This paper is focused on using postcranial skeleton measurements to advance the poorly-studied field of *Apodemus* morphology. These traits are expected to be functionally associated with locomotor performance and therefore good candidates for adaptive evolution. The aims of our study are to (1) analyze morphometric variation of the postcranial skeleton in the majority of *Apodemus* species of the Western Palaearctics, (2) compare morphometric results and available phylogenetic relationships, (3) interpret morphometric patterns in view of the ecological requirements of studied species.

MATERIALS AND METHODS

Studied specimens were collected by the authors and their colleagues during field studies in the Czech Republic and Czech expeditions to the Middle 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 & ŽIŽKOVÁ, 1992 for the characteristic 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 below) due to a very small sample size and that, 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. We studied 265 specimens belonging to the seven species – *A. flavicollis*, *A. witherbyi*, *A. cf. hyrcanicus*, *A. sylvaticus*, *A. uralensis*, *A. mystacinus*, *A. agrarius*. Moreover we use 7 specimens of *A. peninsulae* as a control sample. For details of individual samples (localities, sample size) see Appendix 1.

Most of the studied *Sylvaemus* specimens from the Middle East were determined by biochemical methods (allozymes, 69 specimens, MACHOLÁN et al., 2001) or they were descendants of biochemically determined individuals (11 specimens). Specimens from Sirbasan, Now Kandeh and Asalem were regarded as one *Apodemus* species, because all biochemically determined individuals from these localities belong to only one species. The remaining 18 specimens from the Middle East were identified according to Canonical Variates Analysis based on skull and body measurements (FRYNTA et al., 2001).

Four standard external measurements of each individual were taken using callipers. Subsequently the skeletons were removed and biologically prepared using *Dermestes* larvae. Thirty one postcranial measurements were taken using callipers or a stereomicroscope (see Table 1 for detailed description of the measurements and Appendix 2 for their standard descriptive statistics). To avoid repeated use of the same measurements in our analyses, LTP, LU, LH, LP, LH were used to obtain the following measurements: LTP1 (LTP minus MET) - length of tarsal bones and phalanges, LH2 (LH minus LH1) - length of distal part of humerus, LU1 (LU minus OLE) - functional length of ulna, LP1 (LP minus LP2) - length of ilium (including acetabulum), LT1 (LT minus LT2) - length of proximal part of tibia (to the fusion of tibia and fibula). See Fig. 1 for depiction of the measurements used in our analyses.

TABLE 1
List of measured postcranial characters. C – callipers, SM - stereomicroscope

measured character		symbol	instrument	accuracy (mm)	
external	length of body	LC	C	1	
	length of tail	LCD	C	1	
	length of hind foot	LTP	C	0.1	
	length of ear	LA	C	0.1	
skeletal - forelimb	length of humerus	LH	C	0.1	
	length of proximal part of humerus (to deltoid process)	LH1	SM	0.1	
	width of proximal part of humerus (including deltoid process)	WH1	SM	0.025	
	width of distal part of humerus	WH2	SM	0.025	
	width of distal part of humerus (laterale epicondyle – mediale epicondyle)	WH3	SM	0.05	
	length of ulna	LU	C	0.1	
	length of olecranon (to semilunar notch)	OLE	SM	0.05	
	width of proximal part of ulna and radius	WU	SM	0.025	
	- scapula	length of scapula	LS	SM	0.1
		width of scapula (perpendicular to long axis of spine)	WS1	SM	0.1
		width of scapula (medial angle – inferior angle distance)	WS2	SM	0.05
	- hindlimb	length of femur	LF	C	0.1
		width of proximal part of femur (including third trochanter)	WF1	SM	0.025
		width of distal part of femur	WF2	SM	0.025
width of femoral neck		WF3	SM	0.025	
distance between greater trochanter of femur and femoral head		WF4	SM	0.025	
length of tibia		LT	C	0.1	
length of distal part of tibia (from fusion of tibia with fibula)		LT2	SM	0.1	
width of proximal part of tibia (on tibial crest)		WT1	SM	0.025	
width of distal part of tibia and fibula		WT2	SM	0.025	
length of third metatarsal bone		MET	SM	0.1	
- pelvis	length of coxal bone	LP	SM	0.1	
	length of ischiopubis	LP2	SM	0.05	
	width of ischiopubis	WP1	SM	0.1	
	width of ilium	WP2	SM	0.025	
	length of obturator foramen	LSF	SM	0.05	
	width of obturator foramen	WSF	SM	0.05	
	distance between coxal bones	SW1	SM	0.05	
	width of sacrum	SW2	SM	0.05	
- backbone	length of sixth lumbar vertebra	VBL	SM	0.05	
	width of sixth lumbar vertebra (on transverse processes)	VBW	SM	0.05	

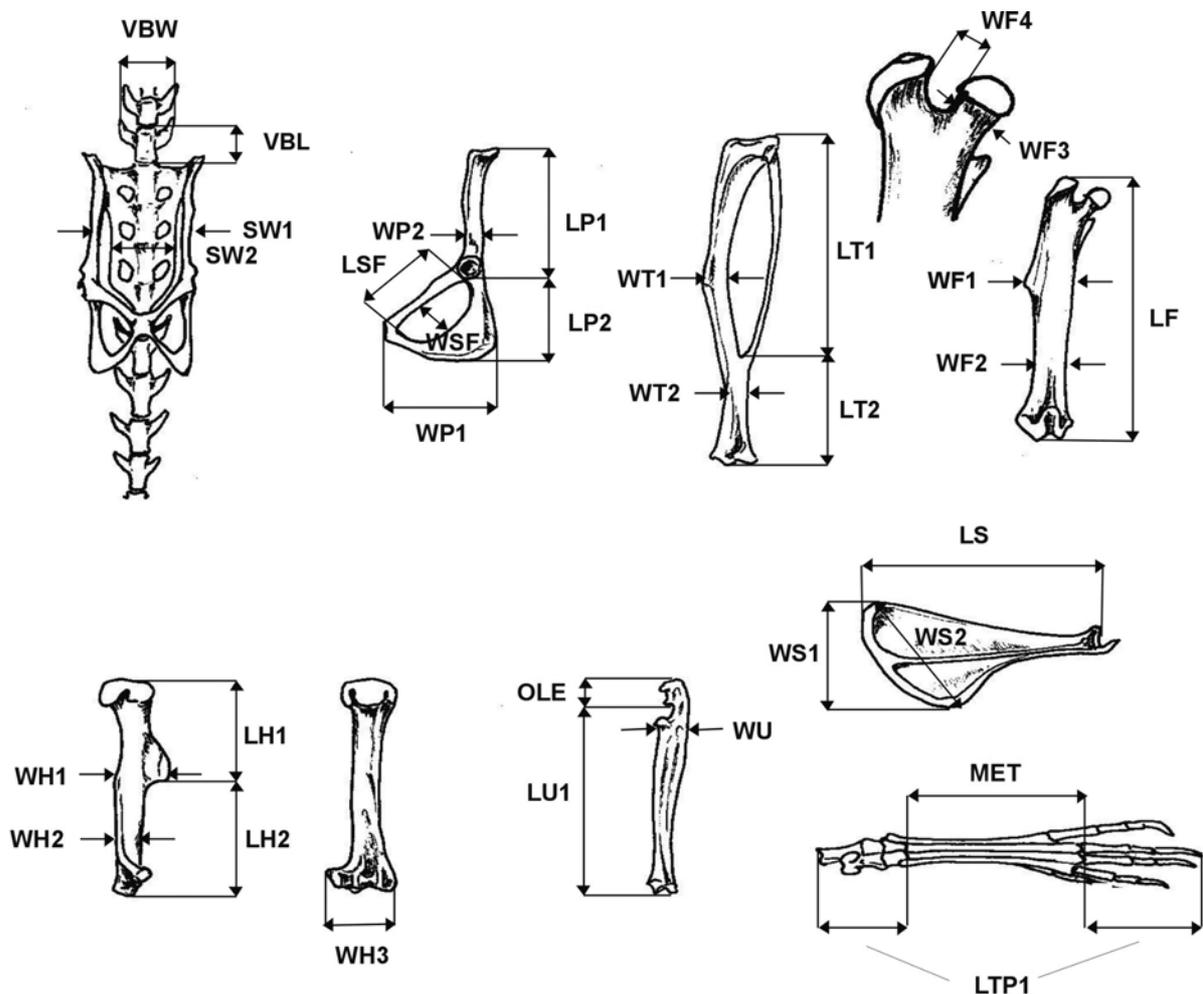


Fig. 1. – Postcranial measurements used in analyses. See Material and Methods and Table 1 for explanation of the measurement abbreviations.

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

The data were log-transformed and missing postcranial values (in case of damaged skeletons) were replaced by those predicted from regression using most correlated variable as an independent factor (assessed according to correlation matrix of all variables). Each population was treated separately to avoid possible differences in allometries. To rule out the effect of growth and size, the Mosimann method of size adjustment (MOSIMANN, 1970) was used in Canonical Variates Analysis (CVA, see below). This data set is therefore referred to as “size-free”. WS1 was omitted in size-free analyses according to the software requirements.

We visually inspected plots of log geometric mean scores (body size) vs. canonical variates scores (CV1-CV3) to detect possible hidden effects of allometries on CVA results. We found consistent allometric relationship for neither within-species nor between-species data. The only partial exception was the case of CV3 scores exhibit-

ing a tendency to positive allometry in between-species comparison.

The log-transformed data were analysed using Principal Component Analysis (PCA). Principal component scores of the first principal component (PC1) 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 CVA subroutine of the STATISTICA Analysis System) between all 10 *Apodemus* samples. UPGMA clustering (STATISTICA Analysis System) was then used to construct a phenetic tree.

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

Classification function resulting from CVA 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.

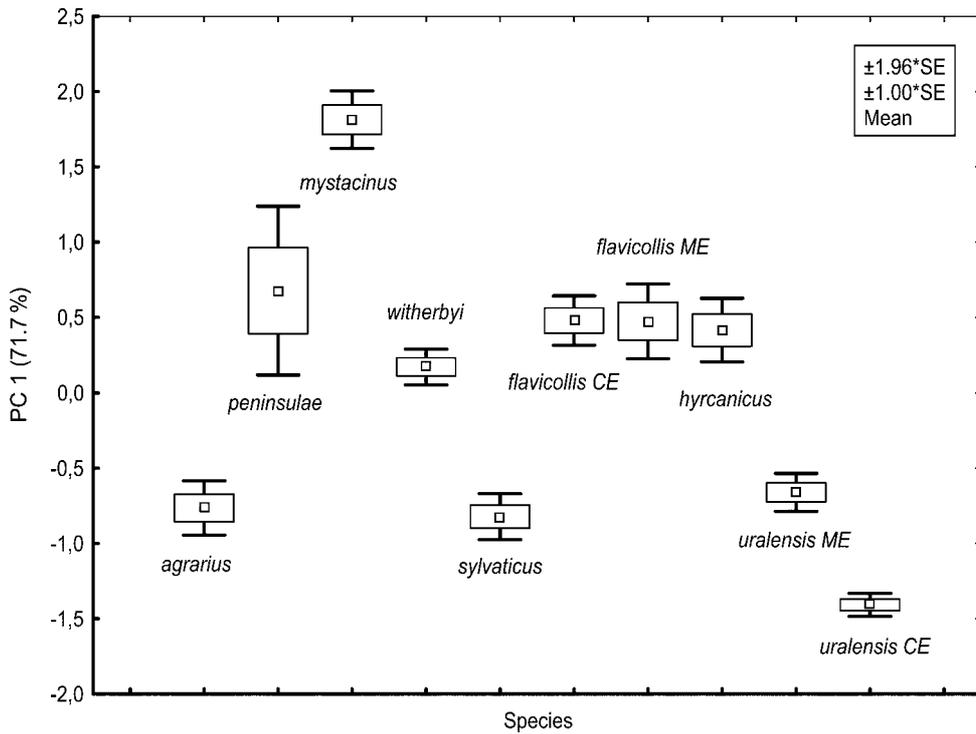


Fig. 2. – Box plots of PC 1 scores derived from original log-transformed data. CE - Central Europe, ME - the Middle East.

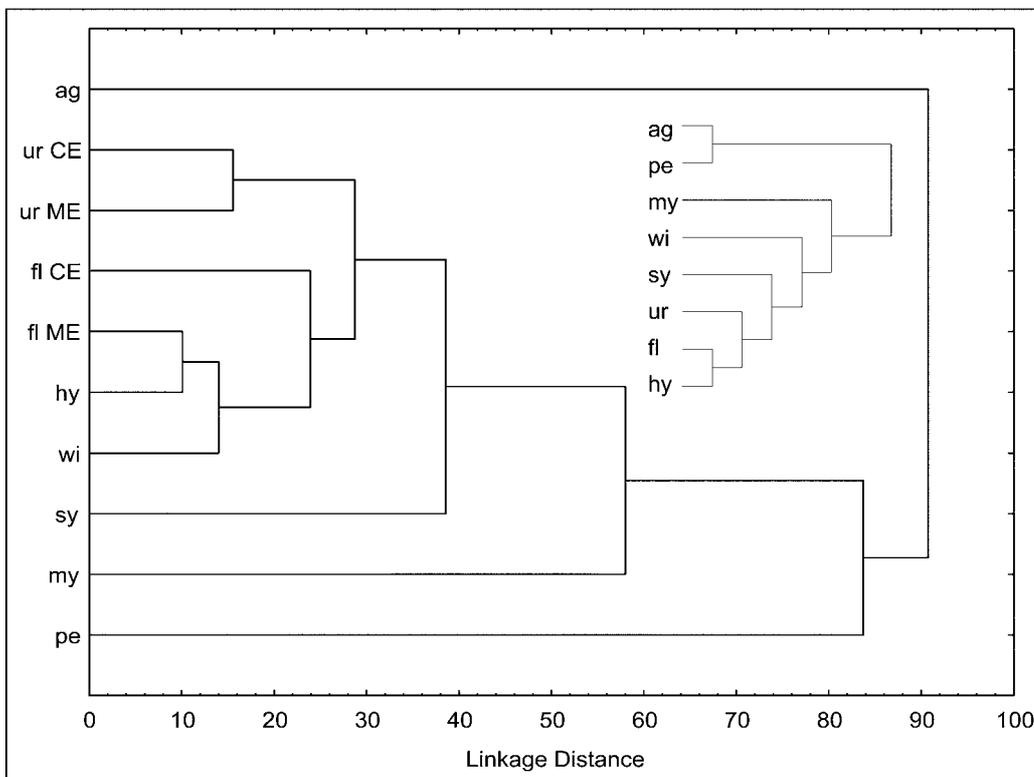


Fig. 3. – Phenetic tree from UPGMA cluster analysis, based on Mahalanobis distances computed from data adjusted by the Mosimann method (size-free data). Genetic tree derived from MICHAUX et al. (2002) and BELLINIA (2004) in the right upper corner. CE - Central Europe, ME - the Middle East.

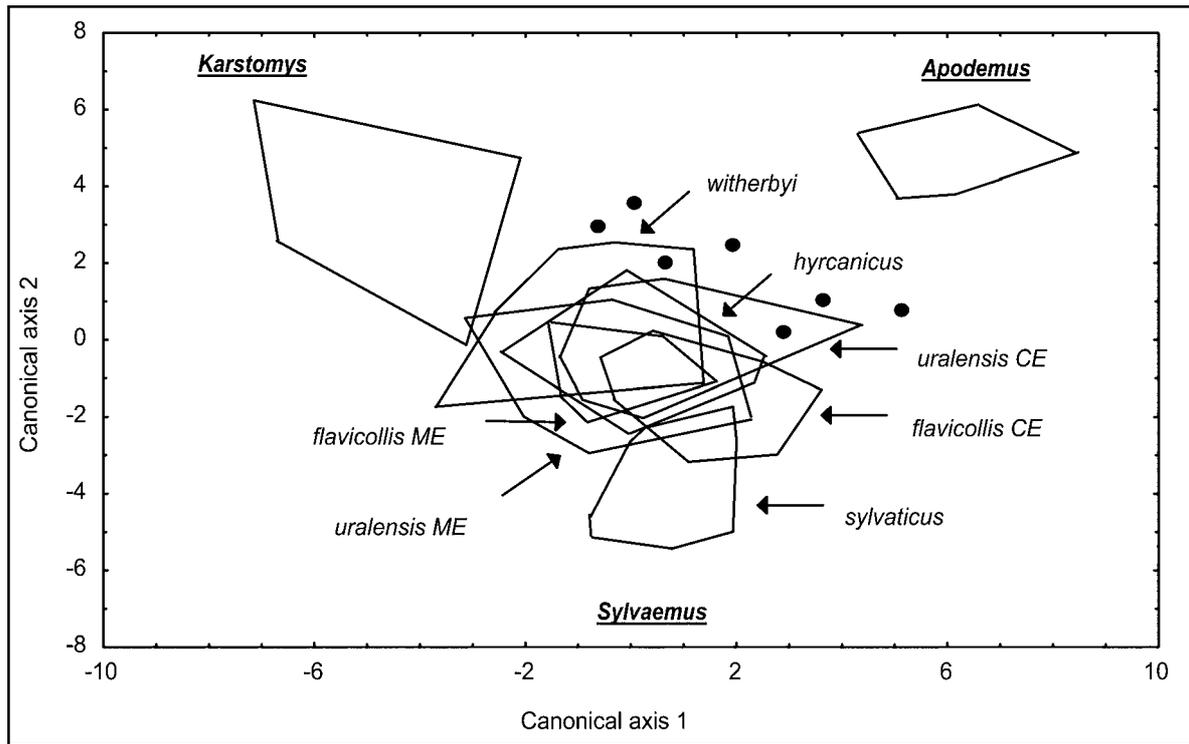


Fig. 4. – Projection of nine studied samples of *Apodemus* species onto the first two canonical variates as derived from data adjusted using the Mosimann method (size-free data). Solid circles depict position of *A. peninsulae* according to classification function resulting from Canonical variates analyses of studied samples. CE - Central Europe, ME - the Middle East.

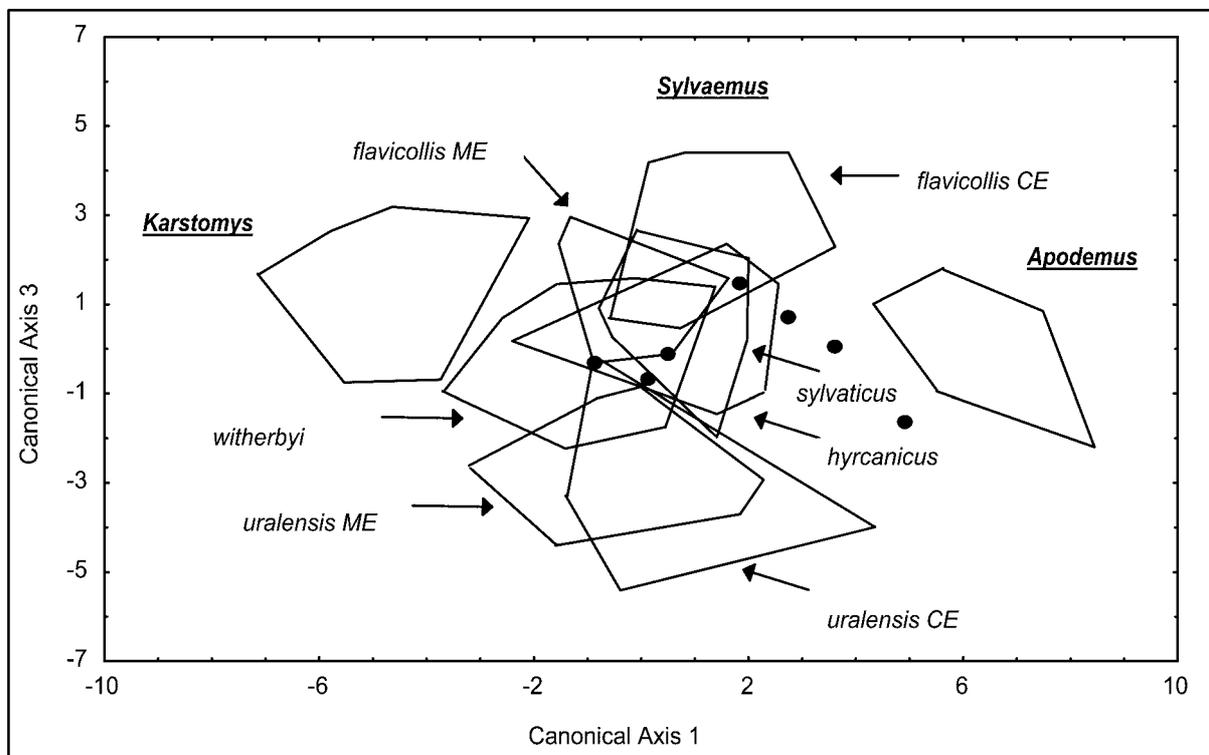


Fig. 5. – Projection of nine studied samples of *Apodemus* species onto the first and third canonical variates as derived from data adjusted using the Mosimann method (size-free data). Solid circles depict position of *A. peninsulae* according to classification function resulting from Canonical variates analyses of studied samples. CE - Central Europe, ME - the Middle East.

TABLE 2

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

	PC1
LC	0.847
LCD	0.853
LTP1	0.857
LA	0.709
LT2	0.783
LT1	0.918
WT1	0.782
WT2	0.886
LF	0.969
WF1	0.896
WF2	0.894
LP2	0.937
LP1	0.867
WP1	0.866
WP2	0.178
LSF	0.797
WSF	0.817
SW1	0.895
SW2	0.859
VBW	0.884
VBL	0.744
WU	0.814
WH1	0.864
WH2	0.859
LS	0.945
WS1	0.879
WS2	0.889
LU1	0.922
LH2	0.873
OLE	0.868
LH1	0.902
WH3	0.908
WF4	0.700
WF3	0.877
MET	0.745

RESULTS

PCA of log-transformed data yielded PC 1 (for loadings see Table 2), which explained 71.7% of the variance ($F=120$, $p<0.001$). It was highly and positively correlated with all traits studied and can be considered as a measure of body size. Along the PC 1 axis, the species studied split into “large” (*A. mystacinus*), “medium” (*A. peninsulae*, *A. flavicollis* from both regions, *A. hyrcanicus*, *A. witherbyi*), and “small” groups (*A. uralensis* from the Middle East, *A. agrarius*, *A. sylvaticus*); *A. uralensis* from central Europe being the smallest one (Fig. 2).

Phenetic comparisons of size-free data (see Appendix 3 for matrix of squared Mahalanobis distances, and Fig. 3 for UPGMA tree) clearly differentiate *A. (Apodemus) agrarius* (with most basal position on phenetic tree), *A.*

TABLE 3

Canonical variate loadings for 34 body and postcranial measurements. Analysis based on data adjusted by Mosimann method (size-free data). See Material and Methods and Table 1 for measurement abbreviations.

	Axis 1	Axis 2	Axis 3
LC	0.209	-0.077	-0.154
LCD	-0.351	-0.059	0.016
LTP1	0.009	-0.266	0.133
LA	-0.186	-0.378	0.041
LT2	-0.207	-0.270	-0.042
LT1	-0.168	-0.153	-0.236
WT1	0.210	0.130	0.061
WT2	0.064	0.043	0.206
LF	-0.148	-0.110	0.018
WF1	-0.061	0.125	0.227
WF2	-0.046	0.142	0.150
LP2	-0.077	0.226	0.116
LP1	0.155	0.160	-0.047
WP1	-0.007	0.169	-0.139
WP2	0.308	-0.197	-0.064
LSF	0.061	0.157	-0.034
WSF	-0.099	0.358	-0.082
SW1	0.077	-0.105	0.176
SW2	-0.045	0.033	0.059
VBW	-0.097	-0.076	0.246
VBL	0.189	0.128	-0.380
OLE	0.086	0.133	0.047
LU1	-0.031	-0.299	-0.172
WU	0.178	-0.034	-0.124
LH1	-0.058	-0.011	-0.072
LH2	0.026	-0.173	-0.043
WH1	0.144	0.018	-0.082
WH2	-0.152	0.158	-0.120
LS	0.106	0.033	-0.189
WS2	0.107	-0.014	-0.271
WH3	-0.073	0.028	-0.101
WF4	-0.002	0.128	0.264
WF3	-0.183	-0.067	0.178
MET	-0.054	-0.505	-0.181

(*Apodemus peninsulae*, *A. (Karstomys) mystacinus* and *A. (Sylvaemus) sylvaticus* (the subsequent branches) from the group of remaining species/populations of the subgenus *Sylvaemus*. Within the latter group, *A. uralensis* and European *A. flavicollis* were the most differentiated, while the samples from the Middle East populations of *A. witherbyi*, *A. hyrcanicus* and *A. flavicollis* clustered together.

We performed CVA on size-free data (Wilks' Lambda=0.00022) in order to evaluate morphological relationships among studied samples (for this analysis the smallest sample, i.e. *A. peninsulae*, was excluded). In total 95% of specimens were correctly classified (the classification was 100% successful in specimens of *A. agrarius*, *A. mystacinus*, *A. sylvaticus* and *A. uralensis* CE; 3 specimens of *A. uralensis* ME were incorrectly classified as *A. uralensis* CE, *A. sylvaticus* and *A. wither-*

byi, 2 specimens of *A. flavicollis* CE as *A. hyrcanicus*, 2 specimens of *A. flavicollis* ME as *A. witherbyi* and 3 specimens of *A. hyrcanicus* as *A. witherbyi*, *A. flavicollis* ME and *A. uralensis* ME). The positions of individual samples in a morphospace of the first three canonical roots are provided in Fig. 4 and Fig. 5 (for loadings see Table 3). *A. (Apodemus) agrarius* and *A. (Karstomys) mystacinus* were clearly separated by Canonical axis 1, while the remaining samples belonging to the subgenera *Sylvaemus* formed a 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 (Fig. 4). Canonical axis 3 further differentiated species of *Sylvaemus*. These species showed gradual separation from *A. uralensis* (negative scores) up to *A. flavicollis* (positive scores).

The classification function resulting from CVA analysis 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*, i.e. species representing the same subgenera (*Apodemus*). For the visualisation of individuals of *A. peninsulae* in morphospace see Figs 4 & 5.

DISCUSSION

Among mammal species, there are differences in the timing of growth among various elements of postcranial skeleton, e.g. the growth of the hind foot is completed much earlier than that of long bones, body and tail (FRYNTA & ŽIŽKOVÁ, 1992; MELIN et al., 2005). This phenomenon may further complicate the interpretation of correlations among studied traits. However, we avoided this potential problem by including only fully grown individuals in our analyses.

Body size itself may play an important role in the adaptive profile of a species, and is sometimes subject to rapid evolutionary change as clearly demonstrated by the phenomenon of island gigantism reported repeatedly in *Apodemus* (ANGERBJÖRN, 1986; LIBOIS & FONS, 1990; LIBOIS et al., 1993; SARÀ & CASAMENTO, 1995). Therefore, it is not particularly surprising that the vast majority of variation we found in postcranial skeleton measurements was explained by the first principal component, and can be attributed to size differences. As this paper is focused on examination of the relationship between morphology and ecology, our discussion will focus solely on the shape component of variance, i.e. on differences in relative size of particular bone segments. 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 molecular phylogeny. Accordingly, the highest degree of morphological differentiation was found among the subgenera *Apodemus*, *Karstomys* and *Sylvaemus*. However, this does not necessarily mean that ecological interpretations of these differences should be excluded (see POE, 2005). In general, related species are more likely to share similar ecological strategies, and thus the distribution of ecologically relevant characters would

often be expected to follow the same phylogenetic pattern. In our case, the subgenus *Karstomys* contains only rock-dwelling species, but *A. agrarius* exhibits a fairly exceptional ecological strategy within the subgenus *Apodemus*. For this reason, we included in our analyses *A. peninsulae*, the other representative of the subgenus *Apodemus* from East Asia, which exhibits ecological requirements similar to those of some European *Sylvaemus* species. Interestingly, 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 closer to the *Sylvaemus* species, but still in the direction towards *A. agrarius*. This seems to support the intuitive view that the ecology of the species is somewhat associated with the shape of its postcranial skeleton.

There is another procedure that may be used to verify the adaptive nature of observed morphological change, i.e. to evaluate agreement of our results with *a priori* hypotheses concerning the relationships between morphology and locomotor performance (see Introduction). Comparison of the characters responsible for observed morphological variation with ecological parameters of studied species, suggests the following functional interpretations. The first canonical root differentiates studied subgenera according to the degree of their subterranean and digging activity. *A. agrarius* possesses relatively short ears and tail (LAU, LCD), short and robust tibia (LT1, LT2, WT1), stout ilium (WP2) and robust ulna (WU), i.e. the characters likely associated with burrowing (i.e. partly subterranean and fossorial) mode of life of this species (e.g. HERÁŇ, 1962a; 1962b; HILDEBRAND, 1985; STEIN, 2000; ELISSAMBURU & VIZCAÍNO, 2004; SAMUELS & VAN VALKENBURGH, 2008). However, contrary to the functional prediction (see DOBRORUKA, 1960; HERÁŇ, 1962a; SCHICH, 1971), *A. agrarius* has relatively long lumbar vertebra (VBL, but see below) and narrow femoral neck (WF3). The opposite is true for *A. mystacinus*, the petricolous, non-burrowing species, for which the long tail (with balance and support function), long tibia, and short lumbar vertebra (YOULATOS, 1999) can be of high importance when moving in a rocky environment (vertical jumping). The *Sylvaemus* species occupy an intermediate position along the first canonical root in accordance with their ecological habits (beside burrows they also frequently use ground and above-ground nests) and behaviour (jumping activity, see results of behavioural tests of FRYNTA (1994) under Introduction), which differ from both *A. agrarius* and *A. mystacinus*. These species form a compact cluster despite supposed variation in the degree of usage of subterranean space among individual species/populations.

The second canonical root separated *Sylvaemus* species (with *A. sylvaticus* in the most extreme position) from *A. agrarius*. This arrangement of studied samples is most likely due to the characters associated with fast terrestrial movement and climbing being opposed by those characters associated with subterranean and digging activity (range of characters, which could not be enforced along Canonical axis 1, recognised as digging – vertical jumping functional sequence; e.g. short LTP1 may be convenient for digging as well as for vertical jumping). The burrowing and digging species – *A. agrarius*, which inhabits

compact vegetation layer hindering fast movement, is characterised by a relatively short ears (LAU), short distal part of hindlimb (LT2, MET, LTP1), short forelimb (LH2, LU1) with long olecranon (OLE) and long (LP2) and broad (WP1) ischiopubis (e.g. HERÁŇ, 1962a; 1962b; HILDEBRAND, 1985; STEIN, 2000; ELISSAMBURU & VIZCAÍNO, 2004; SAMUELS & VAN VALKENBURGH, 2008). While the relatively short post-acetabular part of pelvis (LP2) and long distal elements of the hindlimb (LT2, MET, LTP1) are probably important characters for *Sylvaemus* species inhabiting open microhabitats where fast running or even hopping movement on hindlimbs are used when travelling rapidly (e.g. HERÁŇ, 1962b; SCHICH, 1971). Hopping was reported only in *A. sylvaticus* (DIETERLEN, 1965; NIETHAMMER, 1978) and may be responsible for separation of this species in morphospace along the second canonical axis. Relatively long distal elements of the hindlimb and long forelimbs (with short olecranon) can be further linked with climbing activity (POLK et al., 2000; SAMUELS & VAN VALKENBURGH, 2008; for functional morphology of climbing see also CARTMILL, 1985), which was reported in *A. sylvaticus* and *A. flavicollis*.

The length of lumbar vertebra (VBL) and position of femoral head (WF4) contribute most to the third canonical axis. It differentiates among the *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 Introduction) being in extreme positions. This may be easily interpreted as adaptations: short length of lumbar vertebra found in *A. flavicollis* is possibly associated with vertical leaping (see YOULATOS, 1999 and references therein) and loose femoral head with high degree of lateral movement of the hind limb, the character functionally associated with climbing (DOBRORUKA, 1960).

In conclusion, morphometric examination of postcranial skeleton has revealed considerable variation among subgenera. Interspecific differences usually follow functional predictions associated with ecological habits of species. However, there were found only subtle morphological differences among individual *Sylvaemus* species, in spite of variability of their ecological requirements. This finding may indicate that *Sylvaemus* species possess a majority of generalized morphological features as a result of trade-offs between different habits, which can constrain evolution of special traits on postcranial skeleton (for all species e.g. digging as well as fast running can be of high importance, see also HILDEBRAND, 1985). Ecological diversification of this subgenus can be also explained by body size itself. For proper understanding of the relationship between morphology and ecology, additional comparative data on performance of individual species are urgently required. *Apodemus* species also provide an opportunity to extend our knowledge through additional morphological studies such as e.g. evaluation of character displacement by comparing *Apodemus* populations occurring in sympatry with their counterparts occurring in allopatry (for such a study on cranial measurements see MIKULOVÁ & FRYNTA, 2001).

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Appendix 1 – Origin (localities) and sample size of studied species

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

Apodemus (Sylvaemus) witherbyi: the Middle 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: This species is also referred as *A. hermonensis* Filippucci, Simson, and Nevo, 1989 or *A. iconicus* (Heptner, 1948), see KRYŠTUFEK (2002).

Apodemus (Sylvaemus) cf. hyrcanicus: the Middle 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 80km 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 (Sylvaemus) sylvaticus: Central Europe – 33 specimens from the Czech Republic (Prague).

Apodemus (Sylvaemus) uralensis: Central Europe – 23 specimens from the Czech Republic (southern Moravia: Dyjávovičky); the Middle 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 (Karstomys) mystacinus: the Middle East – 31 specimens from Syria (Quanawat 17, Burqush 1, Slinfeh 12, Sarghaya 1).

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

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

For details of the localities see the following papers: the Middle East - FRYNTA et al. (2001); Prague - MIKULOVÁ & FRYNTA (2001); *Karstomys* - VOHRALÍK et al. (2002).

Appendix 2 – Standard descriptive statistics for 31 postcranial and 4 external measurements (in mm). See Table 1 for measurement abbreviations. CE - Central Europe, ME - the Middle East.

	<i>agrarius</i>		<i>penninsulae</i>		<i>mystacinus</i>		<i>witherbyi</i>		<i>sylvaticus</i>		<i>flavicollis</i> CE		<i>flavicollis</i> ME		<i>hyrcanicus</i>		<i>uralensis</i> ME		<i>uralensis</i> CE	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
LC	94.8	4.27	95.8	8.29	112.2	7.75	98.2	5.61	94.2	4.31	103.4	5.75	100.0	5.67	100.7	7.58	92.7	4.02	89.2	4.00
LCD	76.8	7.06	95.6	14.06	125.0	10.50	101.6	7.28	85.4	5.24	103.9	7.66	104.0	7.81	100.8	6.62	94.7	7.05	81.3	4.08
LTP	18.3	0.90	22.9	1.57	24.6	0.98	21.5	0.90	20.8	0.81	23.5	1.01	22.7	1.30	22.8	0.71	20.9	0.74	18.4	0.73
LA	12.1	0.35	15.3	1.77	18.6	1.69	16.2	0.93	15.7	0.69	17.2	1.05	17.3	1.03	16.6	0.99	14.9	0.72	13.8	1.10
LT	18.41	0.81	22.26	1.29	26.13	1.37	21.72	0.86	20.60	0.91	22.27	0.84	22.42	1.33	22.68	0.86	20.83	0.84	18.84	0.52
LT2	7.29	0.41	8.20	0.32	10.77	0.65	8.52	0.40	8.82	0.53	8.81	0.50	8.84	0.56	8.80	0.41	8.35	0.43	7.36	0.25
WT1	1.75	0.09	2.10	0.24	1.94	0.16	1.66	0.13	1.50	0.14	1.78	0.11	1.87	0.20	1.81	0.17	1.62	0.12	1.36	0.08
WT2	0.94	0.06	1.08	0.08	1.18	0.09	0.98	0.08	0.90	0.08	1.07	0.09	1.08	0.08	1.04	0.09	0.90	0.07	0.82	0.03
LF	16.19	1.14	19.34	1.20	21.79	1.20	18.55	0.93	16.94	0.74	18.75	0.96	19.19	1.32	18.79	1.10	16.81	0.89	15.61	0.53
WF1	2.08	0.19	2.46	0.29	2.72	0.27	2.37	0.23	1.99	0.19	2.27	0.18	2.34	0.18	2.28	0.25	1.95	0.16	1.74	0.09
WF2	1.44	0.11	1.70	0.20	1.90	0.18	1.50	0.14	1.35	0.12	1.57	0.14	1.68	0.16	1.56	0.15	1.40	0.09	1.22	0.08
WF3	0.90	0.06	1.10	0.12	1.33	0.10	1.09	0.09	0.98	0.08	1.14	0.08	1.15	0.07	1.11	0.07	0.98	0.07	0.88	0.04
WF4	0.83	0.12	1.02	0.09	1.08	0.12	0.81	0.14	0.72	0.11	0.90	0.13	0.89	0.10	0.84	0.11	0.69	0.12	0.61	0.08
LP	18.62	1.13	19.86	1.43	22.87	1.56	19.34	1.06	17.21	0.91	19.76	1.29	19.42	1.09	19.32	1.05	17.19	0.94	16.90	0.62
LP2	5.44	0.49	6.21	0.56	7.25	0.75	5.90	0.43	5.08	0.34	6.06	0.42	5.99	0.45	5.85	0.47	5.19	0.37	5.01	0.24
WP1	6.92	0.63	7.38	0.56	8.82	0.76	7.28	0.52	6.51	0.41	7.29	0.70	7.21	0.45	7.12	0.63	6.69	0.47	6.47	0.34
WP2	1.28	0.11	1.50	0.11	1.22	0.09	1.25	0.12	1.26	0.19	1.55	0.16	1.33	0.14	1.36	0.12	1.26	0.13	1.21	0.12
LSF	5.80	0.47	6.01	0.60	7.05	0.61	6.09	0.43	5.17	0.39	6.27	0.61	5.96	0.45	5.95	0.57	5.40	0.43	5.34	0.29
WSF	2.52	0.16	2.43	0.25	3.37	0.27	2.63	0.18	2.10	0.24	2.61	0.21	2.54	0.12	2.71	0.25	2.42	0.19	2.25	0.14
SW1	6.62	0.50	7.37	0.46	8.36	0.78	7.21	0.45	6.88	0.34	7.56	0.54	7.44	0.44	7.36	0.59	6.42	0.43	6.05	0.29
SW2	4.44	0.41	5.05	0.40	5.97	0.56	4.72	0.33	4.56	0.27	4.95	0.37	4.77	0.25	4.78	0.41	4.35	0.34	4.17	0.22
VBW	4.65	0.38	5.70	0.32	6.46	0.55	5.44	0.34	5.03	0.30	5.59	0.37	5.50	0.33	5.50	0.40	4.67	0.36	4.38	0.22
VBL	3.19	0.26	3.35	0.29	3.59	0.30	3.18	0.20	2.88	0.20	3.05	0.19	3.22	0.24	3.20	0.29	3.00	0.23	2.92	0.17
LU	14.28	0.74	16.58	0.78	18.64	0.67	15.88	0.59	15.17	0.53	16.32	0.56	16.64	0.88	16.88	0.67	15.04	0.55	13.80	0.28
OLE	1.95	0.25	2.36	0.19	2.36	0.12	1.99	0.11	1.74	0.13	2.14	0.12	2.07	0.15	2.08	0.12	1.85	0.10	1.71	0.08
WU	1.69	0.10	2.04	0.11	1.98	0.11	1.79	0.14	1.60	0.11	1.92	0.11	1.79	0.09	1.93	0.13	1.69	0.09	1.59	0.08
LH	12.15	0.71	14.00	0.94	15.80	0.80	13.66	0.60	12.63	0.52	13.87	0.67	14.20	0.73	14.25	0.77	12.65	0.54	11.84	0.59
LH1	5.13	0.99	5.84	0.61	6.79	0.46	5.82	0.32	5.11	0.33	5.85	0.45	5.76	0.40	5.92	0.43	5.29	0.36	5.12	0.27
WH1	2.35	0.11	2.97	0.16	2.82	0.22	2.48	0.17	2.22	0.16	2.64	0.18	2.55	0.15	2.56	0.18	2.32	0.10	2.19	0.09
WH2	0.81	0.05	1.16	0.12	1.13	0.09	0.91	0.06	0.79	0.06	0.90	0.07	0.94	0.06	0.92	0.09	0.83	0.04	0.81	0.03
WH3	2.72	0.40	3.38	0.19	3.61	0.14	3.07	0.14	2.63	0.16	3.12	0.15	3.20	0.13	3.23	0.17	2.90	0.20	2.63	0.04
LS	10.25	0.56	11.56	0.50	12.74	0.73	10.95	0.60	10.06	0.38	11.16	0.54	11.29	0.76	10.96	0.56	10.14	0.51	9.66	0.31
WS1	6.91	0.50	7.46	0.53	8.64	0.69	7.69	0.48	6.58	0.46	7.47	0.47	7.50	0.42	7.49	0.61	6.97	0.37	6.51	0.30
WS2	7.57	0.50	7.90	0.72	9.20	0.76	8.36	0.49	7.42	0.49	8.16	0.54	8.48	0.47	8.19	0.63	7.58	0.37	7.21	0.32
MET	7.33	0.38	9.60	0.59	10.02	0.39	8.94	0.33	8.82	0.35	9.58	0.33	9.33	0.41	9.51	0.28	8.90	0.35	7.80	0.31

Appendix 3 - Mahalanobis squared distances computed from data adjusted by Mosimann method (size-free data) .
 CE - Central Europe, ME – the Middle East, ag – *A. agrarius*, ur – *A. uralensis*, sy – *A. sylvaticus*, fl – *A. flavicollis*, wi – *A. witherbyi*,
 hy – *A. hyrcanicus*, pe – *A. peninsulae*, my – *A. mystacinus*

	ag	ur CE	ur ME	my	fl CE	fl ME	sy	wi	hy	pe
ag		75.3	88.0	120.9	81.3	80.1	106.7	77.7	70.4	86.7
ur CE	75.3		14.9	62.5	43.1	38.1	44.2	22.9	27.4	81.5
ur ME	88.0	14.9		51.7	38.1	22.5	36.7	16.8	16.8	75.1
my	120.9	62.5	51.7		68.4	49.1	81.6	37.4	52.4	109.9
fl CE	81.3	43.1	38.1	68.4		22.5	37.0	26.2	20.8	74.4
fl ME	80.1	38.1	22.5	49.1	22.5		30.0	14.6	9.6	72.1
sy	106.7	44.2	36.7	81.6	37.0	30.0		36.6	30.6	115.6
wi	77.7	22.9	16.8	37.4	26.2	14.6	36.6		13.1	74.6
hy	70.4	27.4	16.8	52.4	20.8	9.6	30.6	13.1		64.7
pe	86.7	81.5	75.1	109.9	74.4	72.1	115.6	74.6	64.7	

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