

MORPHOMETRIC DIFFERENCES  
AMONG ROOT VOLE (MURIDAE: MICROTUS OECONOMUS)  
POPULATIONS IN HUNGARY

RÁCZ, G. R.<sup>1</sup>, GUBÁNYI, A.<sup>2</sup>, VOZÁR, Á.<sup>2</sup>

<sup>1</sup>*Museum of Southwestern Biology, University of New Mexico, Biology Department  
Albuquerque, New Mexico, USA, E-mail: raczg@unm.edu*

<sup>2</sup>*Department of Zoology, Hungarian Natural History Museum  
H-1088 Budapest Baross u. 13, Hungary*

*E-mails: gubanyi@zoo.zoo.nhmus.hu, vozar@zoo.zoo.nhmus.hu*

Isolated by hundreds of kilometers from the main population, the southernmost populations of root voles (*Microtus oeconomus*) are vulnerable to extinction in Hungary. Due to restrictions imposed by their protected status, only a limited number of surveys have been conducted to assess the status of the Hungarian populations. Our goal was to understand the historical relationship between Hungarian populations by analyzing morphological skull similarities. We examined skeletal materials deposited in the Hungarian Natural History Museum using geometric morphometric methods. We postulated that greater similarities would be observed among populations that were connected for longer time and smaller populations would exhibit a higher rate of morphological divergence. Individuals from northern Germany were used as an out-group to estimate the ancestral shape of root vole skulls.

Comparison of mandibles and skulls indicates that root vole populations form four regional clusters in Hungary. Two distinct northern groups occupy the Szigetköz and Hanság area. Populations near Lake Balaton form a third, and animals from Kiskunság represent the fourth, highly divergent group. Populations in the Hanság area show the least morphological divergence compared to the out-group indicating that either Hanság was able to support the largest population of root voles or the area served as a center of dispersion for the colonization of other suitable habitats in Hungary.

Key words: root vole, *Microtus oeconomus*, geometric morphometrics, conservation status, metapopulation

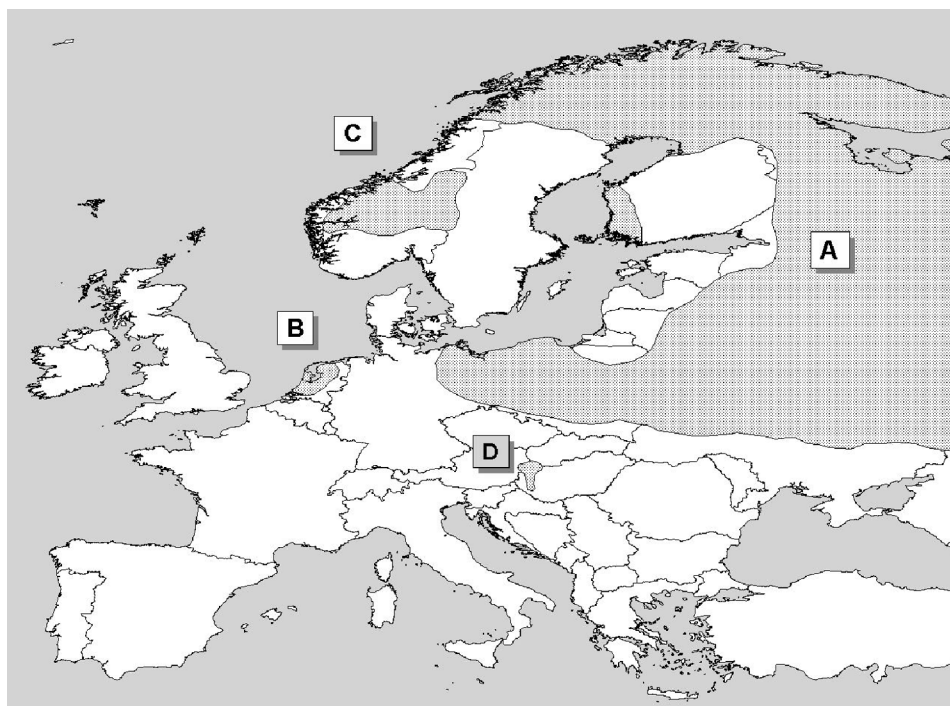
INTRODUCTION

Changing local climate and geographic features are the main regulating forces of the ever changing distribution ranges of mammals (FREY 1992, MACARTHUR 1972). During the colder climate of prehistoric times, the distribution of root voles (*Microtus oeconomus*) extended further south in Europe than presently (JÁNOSSY 1986, REICHSTEIN 1972). Now, the continuous distribution of the species includes the northern part of the Scandinavian Peninsula, areas east of the Elbe River in northern Germany and Poland, but does not extend south of 50° latitude in Europe (Fig. 1) (MITCHELL-JONES *et al.* 1999). The worldwide distribution of the

root vole extends to Asia (Mongolia, Northern China), Alaska and Canada (WILSON & REEDER 1993). Isolated populations of root voles in the Netherlands, Norway, Finland and Central-Europe (Austria, Hungary, Slovakia) are regarded as relict populations from the last glacial period. Based on primarily external measurements and pelt color, 6 subspecies are distinguished in Europe (TAST 1982). Three of the six subspecies represent isolated populations. The subspecies *Microtus oeconomus mehelyi* (ÉHIK, 1928) represents the Central European populations of Hungary, eastern Austria and southern Slovakia.

Prior studies compared local populations of root voles using morphological variation (MARKOWSKI 1980, MARKOWSKI & OSTBYE 1992), protein variation (LANCE & COOK 1998, NADLER *et al.* 1978), DNA fingerprinting (STACY *et al.* 1994), DNA analysis (BRUNHOFF *et al.* 2003, GALBREATH & COOK 2004) and microsatellite DNA variation (VAN DE ZANDE *et al.* 2000).

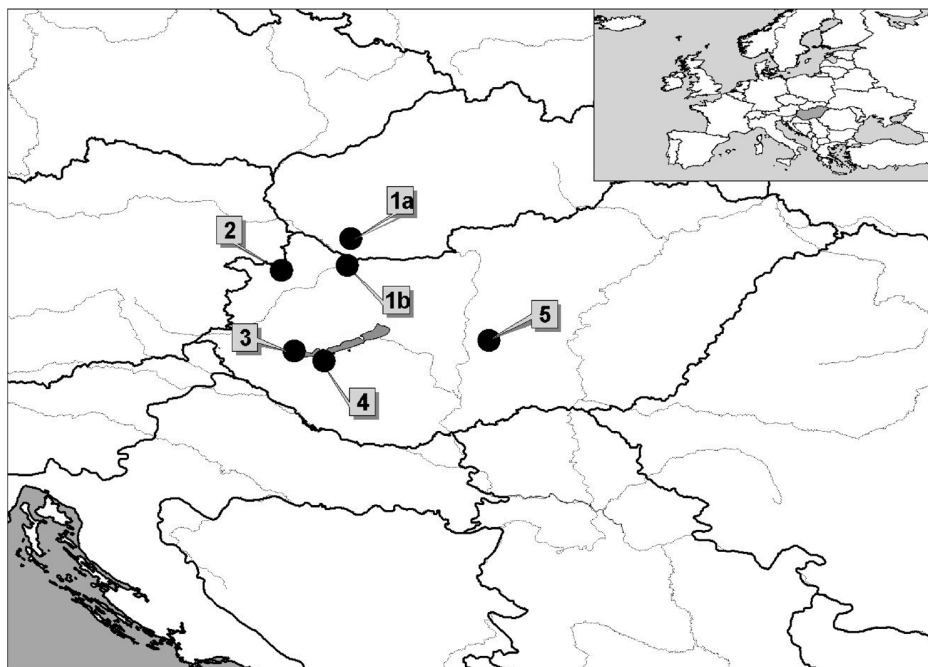
Although root voles have been protected in Hungary since 1974 (RAKONCZAY 1989), habitat loss is still a major threat. The draining of the Hanság basin in the 1950s, canalizing the Zala River, and damming and redirecting the Danube



**Fig. 1.** Distribution of *Microtus oeconomus* in Europe (from MITCHELL-JONES *et al.* 1999) (A= main population, B= Dutch populations, C= Norwegian populations, D= Central European populations)

River in 1990s adversely affected the natural habitats of the root vole. Recent plans for landscape alterations in the Danube region have further increased the concern of regional conservation authorities. Unfortunately, the current status of Hungarian root vole populations is poorly known. Previous studies focused on surveying the distribution of the species in Hungary (ÉHIK 1928, LELKES & HORVÁTH 2000, SZUNYOGHY 1954, TOPÁL 1963). Based on those studies, three distinct regions with scattered populations of root voles have been identified. Populations in the Fertő–Hanság region and Szigetköz are regarded as one geographic unit, populations near Lake Balaton form a second group, and a few populations in the central Hungarian plains are the third geographic group (Fig. 2). Recent studies used microsatellite DNA techniques to monitor the structure of populations based on hair samples of live-trapped animals in Hungary (PAPP *et al.* 2000).

Fragmentation of a previously continuous distribution range has profound implications on the persistence and extinction probability of a species. According to metapopulation theory (HANSKI 1998, HANSKI & GILPIN 1997) species that exist in small isolated populations have higher extinction probabilities than species with a large continuous distribution. The ultimate fate of a species in a fragmented



**Fig. 2.** Collection localities of *Microtus oeconomus méhelyi* specimens used in the study. 1a = Csallóköz (Slovakia), 1b = Szigetköz, 2 = Fertő–Hanság area, 3 = Kis-Balaton, 4 = Dél-Balaton, 5 = Kiskunság)

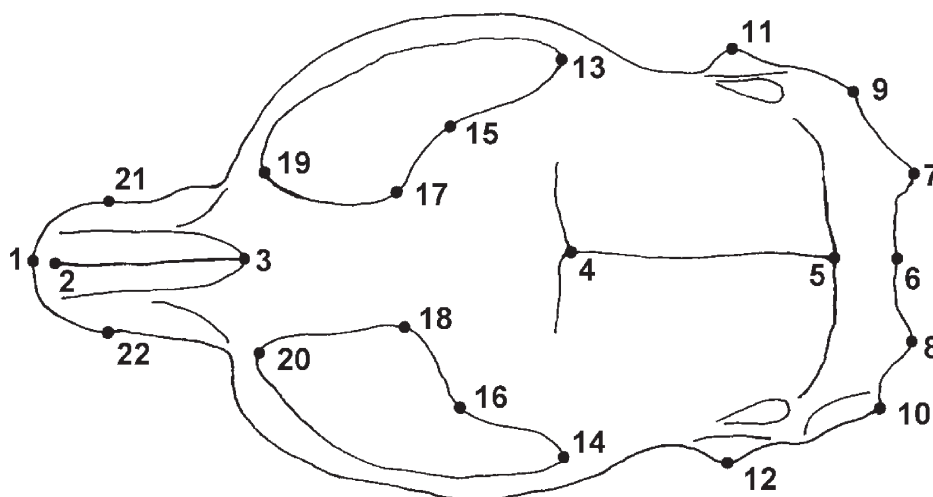
habitat is determined by local population size and the species' ability to colonize suitable but unoccupied habitats. To assess the current conservation status of root voles in Hungary it is important to understand the history and geographic connection among populations. The current study aims to resolve the historical relationship between regional populations of root voles in Central Europe.

### Materials and Methods

All specimens used in this study were pulled from the Mammal Collection of the Hungarian Natural History Museum (HNHM). Only skulls in good condition were photographed and analyzed. Because an intact skull did not necessarily match with an undamaged jaw, the crania and mandibles were analyzed separately. 125 skulls were photographed from dorsal view with a Nikon camera and a professional digitizing card (Table 1). Since there are more characteristic landmarks, many investiga-

**Table 1.** Number of specimens examined from different populations

	mandibles	cranium
1a - Csallóköz/Szigetköz	4	7
2 - Hanság	3	5
3 - Kis-Balaton	157	100
4 - Dél-Balaton	9	4
5 - Kiskunság	2	2
Germany	6	7



**Fig. 3.** Dorsal view of root vole cranium with landmarks

tors would recommend using the ventral view of the skull, yet we decided to photograph the dorsal side because many of the specimens were damaged to a certain degree on the ventral side. Twenty two landmarks (Fig. 3) were marked on the digital picture of the skull using IMAGOES software (DEMETER *et al.* 1996). 181 photographs of the lingual side of left mandibles (Table 1) were taken and subsequently analyzed. Because many of the mandibles had broken coronoid and/or angular processes, only 15 landmarks were marked on these images and several possible landmarks were omitted (Fig. 4). Outside of Hungary, the HNHM has root vole specimens only from Germany. For this reason we measured specimens from Brandenburg, and used this sample as an out-group for comparison. Landmark representations of skulls and mandibles were analyzed in a similar manner: tpsSmall program (ROHLF (1998) and tpsRelw program (ROHLF (1997) were used to calculate centroid size and partial warp scores (Weight matrix) respectively. Individuals were compared based on centroid size and partial warp scores in various statistical tests using STATISTICA software (STATSOFT 1998).

In the first step of analysis, males and females from the same locality were compared to determine whether there are significant shape differences in skull and mandible morphology among sexes. Since there was sufficiently large sample only from one locality (Kis-Balaton, Hungary), males and females were compared only at this single locality. Partial warp scores were compared between males and females using the Hotelling T-test and centroid sizes were compared using t-test.

Because the number of specimens were low at certain localities, differences in centroid size were compared using nonparametric median test. Next, we used the weight matrix and centroid size and ran a discriminant function analysis using these variables to detect morphological differences among subpopulations and to assess whether populations can be distinguished based on skull or mandible shape. tpsRegr program (ROHLF 2000a) were used to show shape differences associated with the first two canonical variates. Finally, landmark representations of skulls and mandibles were averaged from each geographic region in Hungary and consensus configurations were computed using tpsSuper program (ROHLF 2000b). Pair-wise procrustes distances were calculated between group averages using tpsSmall program. Procrustes distance matrix served as the basis to calculate a similarity tree using the UPGMA method in the PHYLIP program package (FELSENSTEIN 1999).

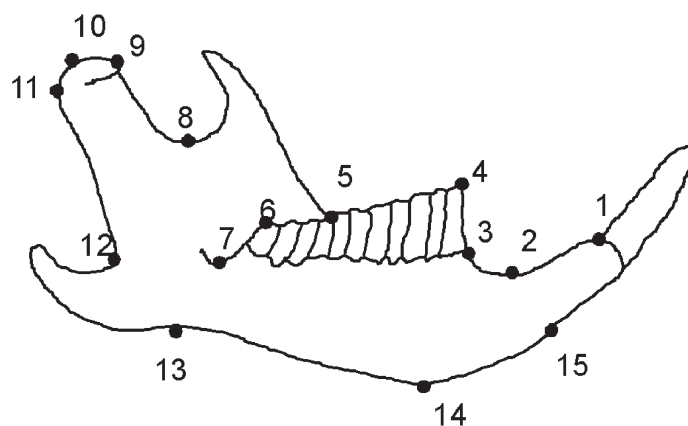


Fig. 4. Lingual view of the left mandible with landmarks

## RESULTS

We found no significant difference in centroid size (cranium  $p < 0.2579$ ; mandibles  $p < 0.775$ ) or in skull shape between sexes using Hotelling's T-test ( $p < 0.9421$ ). Similarly, there was no difference between males and females ( $p < 0.4447$ ) in mandible shape. Because there were no morphological differences among sexes, both sexes were combined and individuals were grouped by geographic localities in subsequent data analyses.

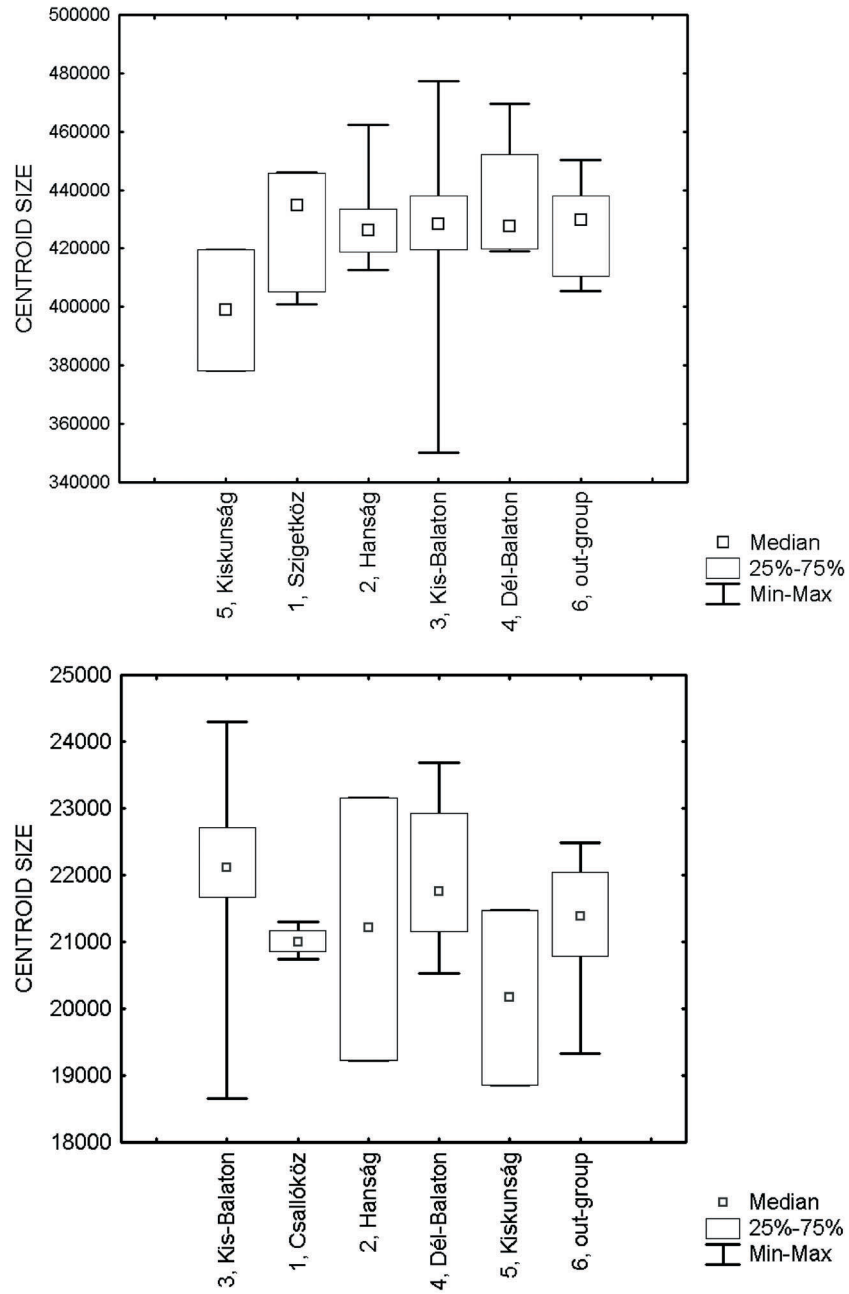
Nonparametric median test did not reject the null hypothesis that there are significant differences among populations in respect of centroid size (cranium  $p < 0.7708$ ; mandible  $p < 0.1784$ ) (Fig. 5). On the other hand, box plots of centroid sizes indicated a potential problem: specimens from the Kiskunság area were rather small, but they were still within the natural size variation shown by other populations (e.g. at Kis-Balaton). Discriminant function analysis on the weight matrix yielded a high level of separation among populations. Based on cranial landmarks, discrimination was strong (Wilks' Lambda = 0.0251,  $p < 0.0000$ ) and group assignment of individuals calculated from discriminant functions was 100 percent correct (Fig. 6a). Calculated from landmarks on the mandibles, discrimination was slightly weaker (Wilks' Lambda = 0.1510,  $p < 0.0000$ ) and the reclassification of individuals was 95 percent correct (Fig. 6b). The Mahalanobis distance matrices gave further insight into the structure of morphological similarity between populations (Table 2 & 3). Based on Mahalanobis distances, the out-group was the most dissimilar from all the other groups. Within the Hungarian groups, the Kiskunság

**Table 2.** Mahalanobis distances among groups based on mandible shape

1a-Csallóköz	0.00					
2 -Hanság	29.85	0.00				
3 -Kis-Balaton	20.36	29.41	0.00			
4 -Dél-Balaton	21.98	31.13	10.44	0.00		
5 -Kiskunság	66.03	45.81	37.60	46.25	0.00	
Germany	35.76	29.64	25.58	19.66	42.33	0.00

**Table 3.** Mahalanobis distances between groups based on cranium shape

1b-Szigetköz	0.00					
2 -Hanság	35.22	0.00				
3 -Kis-Balaton	23.59	27.47	0.00			
4 -Dél-Balaton	42.33	61.29	23.73	0.00		
5 -Kiskunság	46.61	48.36	54.67	85.54	0.00	
Germany	57.08	48.06	53.18	69.82	74.68	0.00



**Fig. 5.** Distribution of centroid sizes among the studied populations calculated from landmarks : a (top) = on the dorsal view of the cranium, b (bottom) = on the mandible. Non-parametric median test failed to reject the idea of significant differences in centroid size among populations

group shows a high level of dissimilarity from the other groups. The procrustes distance matrix calculated from pair-wise comparisons of consensus configurations yielded a slightly more interpretable and detailed pattern of morphometric similarities among populations (Tables 4 & 5). The minimum spanning trees calculated from the morphometric similarity of mandibles (Fig. 7b) and skulls (Figs 7a) show similar topology in general. The two trees agree in grouping Kis-Balaton and Dél-Balaton together. As a result of the morphological dissimilarity of the Kiskunság specimens from any other populations, these specimens are placed on the minimum spanning trees in a position equally far from the other groups.

## DISCUSSION

While molecular techniques, such as microsatellite and mt-DNA analyses, are quite popular among scientists to investigate animal populations, morphometric analysis is still an invaluable tool, especially in cases, where a researcher only has access to older museum specimens. This was the case in our particular study: we compared the skull shape of root voles, a locally endangered species in Hungary, to assess differences among populations. Most of the specimens were collected several decades ago, and since then, two out of the five populations have gone extinct.

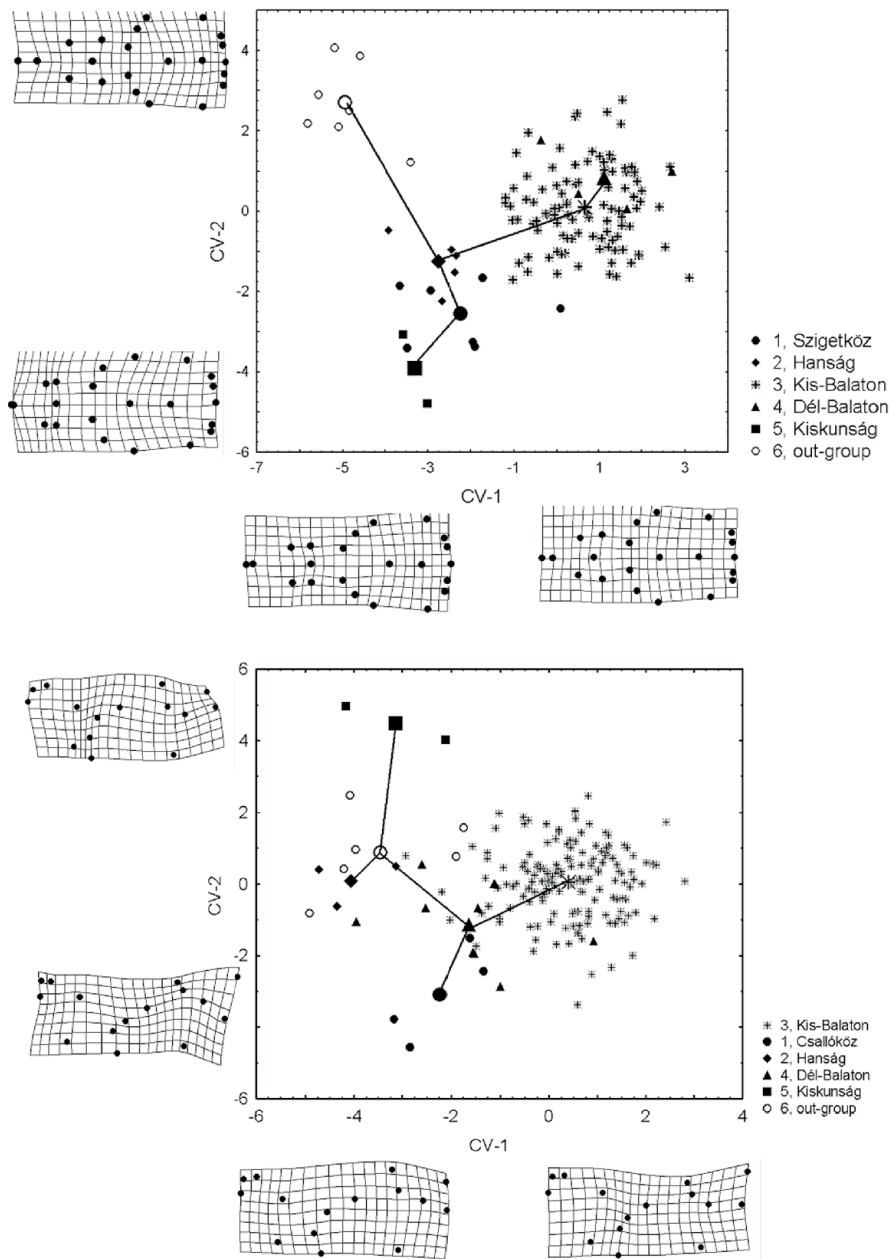
**Table 4.** Procrustes distances based on mandible shape

1a. Csallóköz	0.0000					
2. Hanság	0.0437	0.0000				
3. Kis-Balaton	0.0267	0.0379	0.0000			
4. Dél-Balaton	0.0298	0.0422	0.0193	0.0000		
5. Kiskunság	0.0474	0.0371	0.0345	0.0385	0.0000	
Germany	0.0399	0.0262	0.0278	0.0297	0.0368	0.0000

**Table 5.** Procrustes distances based on cranium shape

1b. Szigetköz	0.0000					
2. Hanság	0.0304	0.0000				
3. Kis-Balaton	0.0278	0.0141	0.0000			
4. Dél-Balaton	0.0306	0.0204	0.0128	0.0000		
5. Kiskunság	0.0428	0.0316	0.0290	0.0314	0.0000	
Germany	0.0570	0.0333	0.0359	0.0362	0.0387	0.0000



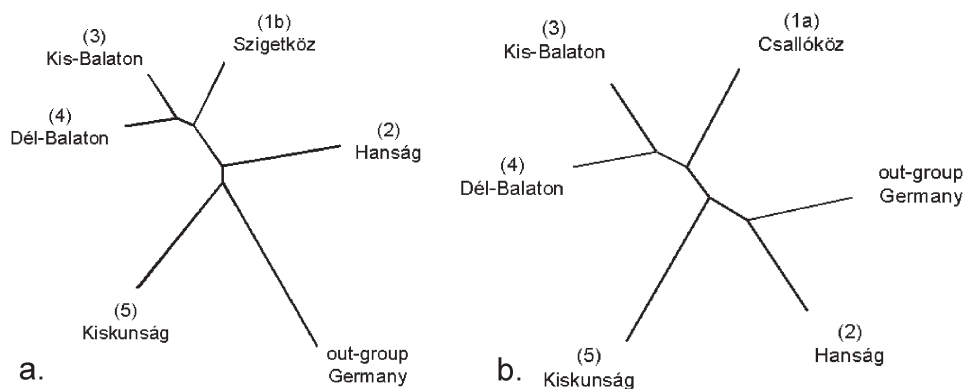


**Fig. 6.** Scatterplots of the first two canonical variate scores calculated from landmarks: a (top) = on the dorsal view of the cranium, b (bottom) = on the mandible. Lines connect the closest laying centroids of each group. Deformation grids were generated using tpsRegr (ROHLF 2000) and show the shape differences associated with the particular canonical variate

While there are doubts among experts whether differences in skull shape reflect genetic divergence or it is caused by environmental effects, previous studies on laboratory stocks of various species of mice demonstrated that cranial morphological features are heritable (ATCHLEY *et al.* 1981). ATCHLEY (1988) estimated that as much as 50% of the morphological variation are of genetic origin. In a recent study MCPHEE (2004) showed that geometric morphometric methods can distinguish laboratory reared populations of *Peromyscus polionotus* from wild and other inbred populations based on cranial morphology. Since the Hungarian populations of root voles are exposed to the same climate, it is a reasonable assumption that differences in skull morphology reflect genetic divergence among populations. While we can never rule out environmental factors, our goal was to use available museum specimens, analyze their morphological variations, and gain some insight into what has happened at the population level in the recent past.

Isolation from the main population increases the chance of local extinction (BURKEY 1995), while isolation and small population size increase the fixation rate of new characters (SACCHERI *et al.* 1998). Divergence from the main population progresses with time and, given a long enough isolation period, speciation may occur (SEDDON *et al.* 2001). Small isolated populations increase local and global biodiversity and they present highly adapted taxa to the local environment, fauna, and flora. Human influence can disrupt the development of natural processes resulting in high extinction rates, a loss of biodiversity, and a lower persistence of local communities against disturbance (TILMAN 1996).

Root voles in the eastern part of the Carpathian Basin represent relict populations of a former glaciation period fauna (JÁNOSSY 1986). Understanding the his-



**Fig. 7.** Minimum spanning tree showing morphometric similarity among populations calculated from pair-wise procrustes distances between consensus configuration of each populations. a = similarities based on the crania, b = similarities based on mandible

tory of these populations is an important step in initiating conservation measures. Establishing new protected areas would help to preserve root vole metapopulation structure in Hungary.

Based on our morphological analysis, the history of the Central European root vole populations can be reconstructed in the following way: the broader distribution range of root voles was split by post-glacial climatic and floral change into two regional populations. One included the Transdanubian area with populations located mostly south and west from the Danube River with a few scattered representatives in northwestern part of the Pannonian Plains. The second region included populations in the Kiskunság, on the Duna–Tisza Interfluvial Plain. Surprisingly, individuals from the Kiskunság area are not the most morphologically divergent when compared to the German population: individuals from the Szigetköz are morphologically more different from the out-group (Tables 4 & 5). This unexpected result indicates that root vole populations existed in satisfactory conditions in the Kiskunság area in the 1950s, when the museum specimens were collected. Several attempts to find root voles have been unsuccessful at the same locations since the 1950s and the root vole is regarded as extinct from this area today.

Specimens from the Kiskunság showed the highest level of similarity to specimens from the Kis-Balaton area. This fact was unexpected, because it was hypothesized that former wetland habitats along the Danube River provided suitable habitats for root voles and populations (Szigetköz and Kiskunság) were once connected along the Danube River. Contrary to previous assumptions, our data suggest that root vole populations were connected for a much longer period through scattered lakes and marshlands south of the Danube River along the line of Kis-Balaton – Balaton and Kiskunság.

Root vole populations on the western edge of the Carpathian Basin experienced further fragmentation during their history. Combining data from the geographic locations and morphological similarities, three separate root vole lineages are distinguishable. All populations in the Hanság area belong to the same independent lineage. Museum specimens from this area show the lowest level of divergence from the German population, perhaps indicating that these populations experienced lower levels of genetic drift. Additionally, individuals from the Hanság appear to be equally dissimilar from individuals of the Kis-Balaton and Szigetköz region, perhaps due to the central geographic position of the Hanság.

Geographically close to the Hanság area, individuals from the Szigetköz/Csallóköz represent another distinct lineage. These individuals show a high level of similarity with the more distant Kis-Balaton populations, while they showed higher level of divergence when compared to specimens from the geographically closer Hanság area. Alarmingly, the Szigetköz populations also show an extensive

divergence from the German out-group. These results may indicate that root vole populations in Szigetköz are in peril due to a high level of fragmentation and low population density.

Populations close to Lake Balaton and in the Kis-Balaton represent the third lineage in the Transdanubian area. Compared to other populations, individuals from Kis-Balaton show a medium level of morphological divergence from the out-group. Populations south of Lake Balaton are peripheral populations with close similarity to individuals from Kis-Balaton. In addition, these individuals show a high level of divergence from the out-group. In the last three decades, humans have exploited natural habitats in the southwestern part of Lake Balaton. The last specimens were captured here in 1955.

In most cases, shape analysis of root vole mandibles and skulls are in concordance. There were only a few instances when the procrustes distance matrices calculated from the two bone structures disagreed. Based on shape analysis of the mandibles, the Kiskunság population experienced a high level of morphological divergence. As a result, the Kiskunság population is placed far from other Central European root vole populations on the similarity tree (Fig. 7b). On the other hand, skull shape indicates a lower level of divergence and animals from the Kiskunság group lie closer to other Hungarian populations (Fig. 7a).

The taxonomic status and the level of divergence of root voles in Central Europe are focal questions for nature conservation authorities. In this study, we used morphological characters to compare several root vole populations. Procrustes distances between out-group and Hungarian individuals were very small (Tables 4 & 5). MARCUS *et al.* (2000) found much higher level of shape difference among species. While MARCUS used representatives of different families, SARA (1996) was able to separate 3 closely related shrew species that were distinguished by much closer procrustes distances. Because the level of morphometric difference is not a good indication of the level of speciation, it would be inappropriate to speculate about the taxonomic status of Central European root voles based exclusively on morphological comparisons. While morphologically these Hungarian animals represented a distinct lineage from the main population, additional genetic analysis would help to assess the level of divergence from other root vole populations.

The most alarming result of our study is the conservation status of various root vole populations in Hungary. The abrupt and recent disappearance of the species from the Kiskunság is a warning sign that stochastic fluctuation can seal the fate of regional populations in a brief period of time. Without an effective conservation program to improve and restore natural wetland habitats in the Szigetköz area, root voles might disappear from this region. The rapid deterioration of natural

root vole habitats of the Szigetköz area since the divergence and canalization of the Danube River is extremely worrisome.

\*

*Acknowledgement* – This research was made possible by support from the Nature Conservation Office of the Ministry of Environment and Water Management, ZooSystem Unlimited Partnership, research grants from the Hungarian Scientific Research Fund (OTKA) project no. T 023876, T 034819 (to ANDRÁS GUBÁNYI), T 037314 (to FERENC MÉSZÁROS) T 3177/91 (to ANDRÁS DEMETER), from the National R&D Programme (The origin and genesis of the fauna of the Carpathian Basin: diversity, biogeographical hotspots and nature conservation significance, project no. 3B023-0-4 and from KAC 020889-0-1/2000 (to ANDRÁS GUBÁNYI). Special thanks are due to the management of Fertő–Hanság National Park and GÁBOR CSORBA (Hungarian Natural History Museum) for their help rendered during the studies.

## REFERENCES

- ATCHLEY, W. R., NEWMAN, S. & COWLEY, D. E. (1988) Genetic divergence in mandible form in relation to molecular divergence in inbred mouse strains. *Genetics* **120**: 239–253.
- ATCHLEY, W. R., RUTLEDGE, J. J. & COWLEY, D. E. (1981) Genetic components of size and shape. 2. Multivariate covariance patterns in the rat and mouse skull. *Evolution* **35**: 1037–1055.
- BRUNHOFF, C., GALBREATH, K., FEDOROV, V., COOK, J. & JAAROLA, M. (2003) Holarctic phylogeography of the root vole (*Microtus oeconomus*): implications for late Quaternary biogeography of high latitudes. *Molecular Ecology* **12**: 957–968.
- BURKEY, T. V. (1995) Extinction rates in archipelagoes: implications for populations in fragmented habitats. *Conservation Biology* **9**: 527–541.
- DEMETER, A., VÁMOSI, J., PEREGOVITS, L. & TOPÁL, G. (1996) An image-capture and data-collection system for morphometric analysis. Pp. 91–102. In MARCUS, L. F., CORTI, M., LOY, A., NAYLOR, G. J. P. & SLICE, D. E. (eds): *Advances in Morphometrics*. NATO ASI Series A Vol. 284. Plenum Press, New York.
- ÉHÍK, J. (1928) Einige Daten zur Säugertierkunde Ungarns. *Annales historico-naturales Musei Nationalis Hungarici* **25**: 195–203.
- FELSENSTEIN, J. (1999) *PHYLIP: Phylogeny Interface Package (Version 3.5)*. University of Washington. Seattle, Washington.
- FREY, J. K. (1992) Response of a mammalian faunal element to climatic changes. *J. Mammalogy* **73**: 43–50.
- GALBREATH, K. & COOK, J. (2004) Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. *Molecular Ecology* **13**: 135–148.
- HANSKI, I. (1998) Metapopulation dynamics. *Nature* **396**: 41–49.
- HANSKI, I. & GILPIN, M. E. (1997) *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California.
- JÁNOSSY, D. (1986) *Pleistocene vertebrate faunas of Hungary*. Akadémia Kiadó. Budapest.
- LANCE, E. W. & COOK, J. A. (1998) Biogeography of tundra voles (*Microtus oeconomus*) of Beringia and the southern coast of Alaska. *J. Mammalogy* **79**: 53–65.
- LELKES, A. & HORVÁTH, G. (2000) The mammalian fauna of Kis-Balaton and population status of root vole (*Microtus oeconomus*). *Somogyi Múzeumok Közleményei* **14**: 359–366.

- MACARTHUR, R. H. (1972) *Geographical ecology; patterns in the distribution of species*. Harper & Row, New York.
- MARCUS, L. F., HINGST-ZAHER, E. & ZAHER, H. (2000) Application of landmark morphometrics to skulls representing the orders of living mammals. *Hystrix* **11**: 27–47.
- MARKOWSKI, J. (1980) Morphometric variability in a population of the root vole. *Acta Theriologica* **25**: 155–211.
- MARKOWSKI, J. & OSTBYE, E. (1992) Morphological variability of a root vole population in high mountain habitats, Hardangervidda, South Norway. *Acta Theriologica* **37**: 117–139.
- MCPHEE, M. E. (2004) Morphological change in wild and captive oldfield mice *Peromyscus polionotus subgriseus*. *J. Mammalogy* **85**: 1130–1137.
- MITCHELL-JONES, A. J., AMORI, G., BOGDANOWICZ, W., KRYSZTOFEK, B., REIJNDERS, P. J. H., SPITZENBERGER, F., STUBBE, M., THISSEN, J. B. M., VOHRALÍK, V. & ZIMA, J. (1999) *The atlas of European mammals*. T & AD Poyser Ltd., London. 484 pp.
- NADLER, C. F., ZHURKEVICH, N. M., HOFFMANN, R. S., KOZLOVSKII, A. I. & DEUTSCH, L. (1978) Biochemical relationships of holarctic vole genera (*Clethrionomys*, *Microtus*, and *Arvicola* (Rodentia: Arvicolinae)). *Canadian J. Zoology* **56**: 1564–1575.
- PAPP, T., GUBÁNYI, A. & RÁCZ, G. (2000) Establishing microsatellite analysis for locally endangered populations of root vole (*Microtus oeconomus*). *Acta zool. hung.* **46**: 259–264.
- RAKONCZAY, Z. (1989) *A Magyarországon kipusztult és veszélyeztetett növény- és állatfajok*. Akadémia Kiadó, Budapest.
- REICHSTEIN, H. (1972) Ein Nachweis der Nordischen Wühlmaus, *Microtus oeconomus* (Pallas, 1776) aus dem vorgeschichtlichen Nordwest-Deutschland. *Zeitschrift für Säugetierkunde* **37**: 98–101.
- ROHLF, F. J. (1997) *tpsRELW (Version 1.16)*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.
- ROHLF, F. J. (1998) *tpsSMALL (Version 1.19)*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.
- ROHLF, F. J. (2000a) *tpsREGR (Version 1.22): Thin-Plate Spline Regression*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.
- ROHLF, F. J. (2000b) *tpsSuper (Version 1.07)*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.
- SACCHERI, I., KUUSSAARI, M., KANKARE, M., VIKMAN, P., FORTELIUS, W. & HANSKI, I. (1998) Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**: 491–494.
- SARA, M. (1996) Landmark based morphometrics approach to the systematics of Crocidurinae: Case study on endemic shrews *Crocidura sicula* and *C. canariensis* (Soricidae, Mammalia). Pp. 335–344. In MARCUS, L. F., CORTI, M., LOY, A., NAYLOR, G. J. P. & SLICE, D. E. (eds): *Advances in Morphometrics*. NATO ASI Series A vol 284. Plenum Press, New York.
- SEDDON, J. M., SANTUCCI, F., REEVE, N. J. & HEWITT, G. M. (2001) DNA footprints of European hedgehogs, *Erinaceus europaeus* and *E. concolor*: Pleistocene refugia, postglacial expansion and colonization routes. *Molecular Ecology* **10**: 2187–2198.
- STACY, J. E., REFSETH, U. H., THORESEN, M., IMS, R. A., STENSETH, N. C. & JAKOBSEN, K. S. (1994) Genetic variability among root voles (*Microtus oeconomus*) from different geographic regions: populations can be distinguished by DNA fingerprinting. *Biol. J. Linnean Soc.* **52**: 273–286.
- STATSOFT, I. (1998) *Statistica for Windows*. Computer Program Manual. Tulsa, OK.
- SZUNYOGHY, J. (1954) Adatok a *Microtus oeconomus* méhelyi Éhik elterjedésének, halló- és pénis-csontjának ismeretéhez. *Állattani Közlemények* **64**: 225–230.

- TAST, J. (1982) *Microtus oeconomus* (Pallas, 1776) – Nordische Wühlmaus, Sumpfmaus. Pp. 374–396. In NIETHAMMER, F. K. J. (ed.): *Handbuch der Säugetiere Europas*. Akademische Verlagsgesellschaft, Wiesbaden.
- TILMAN, D. (1996) Biodiversity: Population versus ecosystem stability. *Ecology* **77**: 350–363.
- TOPÁL, G. (1963) Újabb adatok a *Microtus oeconomus* méhelyi magyarországi előfordulásához és a Tisza menti (Sasér) előfordulás cáfolata. *Vertebrata Hungarica* **1–2**: 159–165.
- VAN DE ZANDE, L., VAN APELDOORN, R. C., BLIJDENSTEIN, A. F., DEJONG, D., VAN DELDEN, W. & BIJLSMA, R. (2000) Microsatellite analysis of population structure and genetic differentiation within and between populations of the root vole: *Microtus oeconomus* in the Netherlands. *Molecular Ecology* **9**: 1651–1656.
- WILSON, D. E. & REEDER, D. M. (1993) *Mammal Species of the World: A Taxonomic and Geographic Reference*. 2nd. ed. Smithsonian Institution Press.

Revised version received March 24, 2005, accepted May 9, 2005, published June 30, 2005