# *Microtus (Microtus) nivaloides* from the Somssich Hill 2 site (southern Hungary): an Early Pleistocene forerunner of modern 'true' *Microtus* voles revealed by morphometric analyses

**Piroska Pazonyi[a,*], Attila Virág[a], János Podani[b,c], József Pálfy[a,d]**

[a] MTA-MTM-ELTE Research Group for Paleontology, POB 137, Budapest, H-1431 Hungary

[b] Department of Plant Systematics, Ecology and Theoretical Biology, Eötvös Loránd University, Pázmány Péter sétány 1/C, Budapest, H-1117 Hungary

[c] Ecology Research Group, Hungarian Academy of Sciences, Budapest, Hungary

[d] Department of Geology, Eötvös Loránd University, Pázmány Péter sétány 1/C, Budapest, H-1117 Hungary

[*] Corresponding author. E-mail address: pinety@gmail.com (P. Pazonyi)

## Abstract

Voles are among the most common and abundant rodents in Central Europe, represented by several species of *Microtus* and other genera. This group is also common in Pleistocene fossil assemblages. However, the taxonomy of fossil finds, largely based on lower first molars, is fraught with problems and opinions of various authors often diverge, hampering phylogenetic inferences and reconstruction of lineages which led to the extant species. To help solve taxonomic incongruence, we carried out morphometric analyses on the abundant late Early Pleistocene finds from the exceptionally rich site of Somssich Hill 2 (Villány Mts., southern Hungary), complemented with less numerous but also well-dated and nearly coeval material from nearby sites Villány 6 and 8, as well as Kövesvárad from northern Hungary. Both traditional multivariate morphometric methods (cluster and discriminant analyses) and geometric morphometric techniques (landmark and Procrustes analyses) were applied. First

lower molars of well-established recent taxa from zoological museum collections were also included in the analyses, both to assess their degree in intraspecific morphological variability to inform delineation of fossil taxa, and to compare morphologies of fossil and recent taxa to establish phylogenetic relationships. Morphometric analyses and comparison with the range of variability of modern taxa reveal that the material from Somssich Hill 2 represents a single species, *Microtus nivaloides*, whereas specimens from the somewhat younger sites Villány 6 and 8 belong to *M. nivalinus*. Paleoecology of the accompanying taxa in the fossil assemblages suggests differences in their habitat: *M. nivalinus* preferred more open vegetation, whereas *M. nivaloides* was restricted to forested areas. Geometric morphometric analyses together with modern taxa defined a morphospace where the consensus shape of *M. nivaloides* is centrally located, supporting the hypothesis that it represents the ancestor of modern *Microtus* (*Microtus*) species and forms part of a lineage which led to the *M. arvalis-agrestis* group. On the other hand, morphological similarities suggest a split lineage and phylogenetic relations of late Early Pleistocene *M. nivalinus* and the recent *M. oeconomus.* The emergence of 'true' *Microtus* species stems from the radiation initiated around 1.0–0.9 Ma, an important phase in vole evolution revealed by the rich finds from Somssich Hill 2 and other sites.

**Keywords:** *Microtus*, Pleistocene, Villány Mountains, morphometric analysis, geometric morphometrics, phylogeny

## 1. Introduction

The karst fissure of the Somssich Hill 2 site (situated near the village of Villány, southern Hungary) is one of the richest late Early Pleistocene vertebrate localities of Central Europe. The clay-rich fissure fill yielded an exceptionally rich vertebrate assemblage which includes

remains of fish, anurans (Szentesi, 2014, 2016), reptiles, birds and mammals (Jánossy, 1986, 1990). The remarkably diverse small mammalian fauna contains shrews (Botka and Mészáros, 2014), hamsters (Hír, 1998), mice (Hír, 1998), dormice (Striczky and Pazonyi, 2014) and voles (Jánossy, 1983, 1990; Pazonyi et al., 2013). The most common elements of the fauna are voles and lemmings. More than 15,000 first lower molars ($m_1$) were identified from the 50 layers of the fissure fill.

Among the voles, remains of *Microtus* are the most abundant (more than 6000 $m_1$ specimens), accompanied by *Mimomys*, *Pliomys*, and *Myodes*. According to Jánossy (1990), six species of three subgenera were identified within the genus *Microtus*: the advanced *M. (Allophaiomys) pliocaenicus*, *M. (Terricola) gregaloides*, *M. (T.) arvalidens*, *M. (Microtus) arvalinus, M. (M.) gregalis, M. (M.) ratticepoides*. In addition, Jánossy (1999) mentioned *M. (M.) nivaloides* as well. Based on the co-occurrence of *Allophaiomys* and 'true' *Microtus* species, the age of the locality falls into the latest Early Pleistocene (approximately 1.0–0.9 Ma), using the chronology of Maul and Markova (2007). The assemblage is assigned to the *Mimomys savini-Mimomys pusillus* Biozone of the local biochronological system of Kordos (1994).

This interval coincides with one of the most important radiation events for the voles, which occurred within the *Allophaiomys–Microtus* lineage, and subsequently led to the modern diversity of this group (Rabeder, 1981). This event was most plausibly triggered by the extension of grasslands due to a progressive climate change initiated at the beginning of the Pleistocene, approximately 2.6 Ma (Kolfschoten and Markova, 2005). However, details of the Pleistocene evolution of vole lineages are not fully understood. The key issues are the reconstruction of evolutionary lineages leading to modern vole species and constraining the age of splitting of these lineages (Van der Meulen, 1973; Rabeder, 1981; Nadachowski, 1991;

Maul and Markova, 2007). Establishing the vole phylogeny is hampered by taxonomic confusion of several closely related nominal species of high morphological similarity.

In order to improve the reliability of vole taxonomy, the main aims of this work are to develop a new method which combines traditional and geometric morphometric approaches, and to demonstrate its utility in the comparison of various fossil and extant species of the genus *Microtus*. The primary focus of the present study is to prove that the morphology of the previously described four 'true' *Microtus* voles from the Somssich Hill 2 site can be interpreted as a single species, which we think is *M. nivaloides*, the oldest known *Microtus (Microtus)* species in the region. Thus we analysed all 'true' *Microtus* lower first molars that were used by Jánossy (1990, 1999). The large sample size (more than 1,500 $m_1$) allowed us to analyse its morphological differences from and phylogenetic relationship with both voles from some nearly contemporaneous sites (Villány 6 and 8, and Kövesvárad) and modern taxa. The emergence of 'true' *Microtus* species can be regarded as the result of the radiation initiated around 1.0–0.9 Ma from a hypothetical ancestor similar to *M. nivaloides* at the Somssich Hill 2 site.

## 2. Geological setting and biostratigraphic framework

The studied vole material was found at four broadly contemporaneous localities in Hungary: Somssich Hill 2, Villány 6, Villány 8, and Kövesvárad. The first three localities are situated in the Villány Mountains (southern Hungary), near the village of Villány, whereas Kövesvárad is located in the Bükk Mountains (northeastern Hungary) (Fig. 1). The material was recovered from reddish brown clay or yellowish brown silt infillings of karst cavities. The karstified limestone is Middle Triassic in age at Kövesvárad and Late Jurassic at the sites of Villány 6 and 8, and Somssich Hill 2.

Somssich Hill 2 is an 8 m deep karst cavity with a surface diameter of 5 m, situated on the top of Somssich Hill, west of the village of Villány (Fig. 1). The infilling sediment is reddish brown clay at the bottom of the sequence (below 4 m), whereas it grades upwards into yellowish brown silt (Jánossy, 1990). Several interbeds of varying thickness with limestone clasts encrusted by calcite occur between depths of 2.5 and 5.0 m.

The age of Somssich Hill 2 locality is latest Early Pleistocene (approximately 1.0–0.9 Ma), equivalent of the *Mimomys savini-Mimomys pusillus* Biozone, based on the co-occurrence of advanced *Allophaiomys* and 'true' *Microtus* species together with *Mimomys savini* and *Mimomys pusillus*. Similar vole faunas have been found from Ukraine (Bolshevik 2-III, Protopopovka 2, Tikhonovka 2, Karay Dubina; Rekovets and Nadachowski, 1995) and Bulgaria (Subzone B2 of the Kozarnika Cave; Popov and Marinska, 2007) in Eastern Europe, from Poland (Zalesiaki 1; Nadachowski, 1990a) in Central Europe, as well as from Spain (the lower layers of Gran Dolina in Atapuerca; Antoñanzas and Cuenca Bescós, 2002) in Southern Europe. (Fig. 2).

Villány 6 is a north-south trending, vertical karst fissure of very large size, which is exposed in the southern wall of the limestone quarry at Templom Hill (Fig. 1). The infilling sediment is cherry-coloured terra rossa, which is penetrated by sheets of recrystallized calcareous precipitate (Kretzoi, 1956; Jánossy, 1986). Based on the occurrence of *Mimomys pusillus*, *Mimomys savini*, and the absence of *Allophaiomys*, the vole fauna is slightly younger than that of Somssich Hill 2, but it can also be assigned to the *Mimomys savini-Mimomys pusillus* Biozone (Kordos, 1994) (Fig. 2).

Villány 8 is a karst cavity connected to a fissure system, also exposed in the southern wall of the abandoned limestone quarry at Templom Hill, north of Villány (Fig. 1). The lower layers of the infilling sediment are reddish brown clays with calcareous interbeds, whereas

upwards it grades into yellowish brown silt, similarly to the Somssich Hill 2 site (Jánossy, 1986).

Villány 8 is the stratotype section of the Templomhegy Phase within the Biharian Stage of the local biochronological system (Kretzoi and Pécsi, 1982; Jánossy, 1986). The beginning of the Templomhegy Phase is closely correlated with the Early-Middle Pleistocene boundary, and regionally marked by environmental change which led to increasing forest cover (Fig. 2). The vole fauna is slightly younger than in Villány 6, it was assigned to the *Mimomys savini* Biozone based on the absence of *Allophaiomys* and *Mimomys pusillus* (Kordos, 1994). Similar assemblages are known, among others, from Great Britain in Western Europe (West Runton; Maul and Parfitt, 2010) and from Poland in Central Europe (Kozi Grzbiet; Nadachowski, 1985). Those sites postdate the Matuyama-Brunhes reversal, with an approximate age between 780–650 ka (Maul and Parfitt, 2010).

The fossiliferous locality at Kövesvárad is a 5 m high and 3 m wide karst cavity situated east of the village of Répáshuta (Fig. 1). The vole material was recovered from the orange and reddish brown clay infilling (Jánossy, 1963, 1986). Based on the occurrence of *Mimomys savini* and the absence of *Allophaiomys* and *Mimomys pusillus*, the age of the site was correlated with Villány 8, and assigned to the *Mimomys savini* Biozone (Kordos, 1994) (Fig. 2).

## 3. Material

A total of 587 teeth were selected from more than 1,500 'true' *Microtus* lower first molars ($m_1$) from the Somssich Hill 2 site. Only those undamaged specimens were chosen, on which all of the characters discussed below were observable. From the other fossil localities included in the present study (Villány 6, Villány 8 and Kövesvárad), fewer *Microtus (Microtus)* specimens were available (26, 178 and 8 specimens, respectively). The material

analysed from Villány 6 and 8 includes several specimens previously studied and reported by Van der Meulen (1973). The specimens from Somssich Hill 2 and Kövesvárad are housed in the Department of Paleontology and Geology, Hungarian Natural History Museum (HNHM), Budapest, whereas the material from Villány 6 and 8 is stored at the Department of Geological and Geophysical Collections, Geological and Geophysical Institute of Hungary (GGIH), Budapest.

First lower molars belonging to four recent species, *Microtus agrestis* (354 specimens), *M. arvalis* (628 specimens), *M. oeconomus* (444 specimens), and *Chionomys nivalis* (96 specimens) were also measured and included in the analyses for comparison. The latter specimens are stored in the Mammalia Collection, Department of Zoology of the HNHM. The numbers express $m_1$ specimens rather than individual animals, because both left and right molars were used and counted in this study.

**4. Terminology of vole first lower molars**

Voles have very distinctive, intricately folded molar enamel which encapsulates the dentine core of the tooth. The anterior ending of a first lower molar is referred to as anterior cap (AC), whereas the posterior loop (PL) is the talonid. The alternating indentations (or re-entrant angles, RA) of enamel on both sides of a molar separate the triangles (or the so called 'Pitymys rhombus', in which case buccal and lingual triangles are not sufficiently isolated). The indentations are filled with cementum in most cases (Van der Meulen, 1973). The outward folds of the triangles are referred to as salient angles (SA). The triangles are labelled from posterior to anterior direction, thus the most posterior triangle on the lingual side of a molar is called T1. The AC together with all triangles in front of T3 are termed the anteroconid-complex (ACC). The narrow separation between the T4-T5 and the T6-T7 triangles is called neck (Fig. 3).

With the successive infolding of the anterior cap, new triangles emerged posterior to the newly developing cap in several vole lineages during evolution. Due to this process, the occlusal outline (especially in case of the lower first molar) varies among the taxa, and is usually appropriate for identification at the species level (Hillson, 2005). In addition, the inner structure and other visible features of enamel (such as thickness changes and stripes which may be missing on the sides of the tooth downwards from the crown) are also key features to identification (Mayhew, 2009).

## 5. Methods

### *5.1. Data acquisition*

In order to carry out standard morphometric measurements and to record geometric coordinates of landmark ~~points~~ which describe the outline of molar enamel sufficiently, groups of 20 to 30 teeth were fixed with a reusable putty-like pressure-sensitive adhesive on a small disk installed on a ball joint. Photomicrographs of the occlusal surfaces were taken using a Canon EOS 450D digital camera fixed with a modified T2 adapter into the socket of the right ocular of a Nikon SMZ445 stereomicroscope. Each surface was brought to a horizontal position with the rotation of the disk before taking the photographs. The same protocol was used for all photographs. In this way, a large number of images can be made quickly and efficiently.

The landmark (LM) and ~~sliding~~ semi-landmark (SLM) ~~points~~ (22 and 16, respectively) were digitized directly on the photographs using the *tpsDig* software (available at http://life.bio.sunysb.edu/morph/). Landmarks correspond to the salient and re-entrant angles as well as the most anterior point of the cap and the most posterior point of the talonid, whereas semi-landmarks were defined at inflexions or slight curvature changes between the LM points. In the lack of such features, SLM points were digitized as midpoints between the

neighbouring LM points. In forms similar to *M. oeconomus*, the fourth buccal re-entrant angle (BRA4) is missing or vestigial, therefore the landmark points representing BSA4, BRA4, and BSA5 (LM4, LM3, and LM2, respectively) were evenly distributed between the most anterior point of the molar (LM1) and the point superimposed to BRA3 (LM5) (Fig. 4 shows the LM and SLM points).

*5.2. Traditional morphometric measurements*

Traditional morphometric measurements were made using the raw coordinates of the LM and SLM ~~points.~~ In order to obtain results which are comparable with the conventional measurements in the literature (Van der Meulen, 1973, Nadachowski, 1982, 1991, Rekovets and Nadachowski, 1995, Petruso et al., 2011) the following variables were used in this study (Fig. 5):

**L**: The maximum length of the occlusal surface, which is defined as the distance between LM1 and LM11, and measured along the longitudinal axis of the molar from the most anterior part of the anterior cap to the most posterior point of the talonid.

**A** (equivalent to 'a' in Van der Meulen, 1973 and Rekovets and Nadachowski, 1995): The length of the anteroconid-complex, defined as the distance between LM1 and LM7, measured along the longitudinal axis of the molar from the anterior tip of the molar to the most anterior point of BRA2.

**A2**: The length of the anterior part of ACC (AC and T6-T7 triangles) on the buccal side of $m_1$, defined as the distance between the LM1 and LM5 points, measured along the longitudinal axis of the molar from the anterior tip of the molar to the most anterior point of BRA3.

**W** (equivalent to '$W_1$' in Nadachowski, 1982): The width of the posterior part of the ACC, defined as the distance between the LM6 and LM18 points, measured from the outermost point of BSA3 to that of LSA4.

**D** (equivalent to '$B_2$' in Nadachowski, 1982, 'd' in Van der Meulen, 1973 and Rekovets and Nadachowski, 1995): The width of the infolding between the AC and the remaining part of the ACC was calculated from the coordinates of LM3 and LM21 points. Alternatively, it can be interpreted as the distance between BRA4 and LRA5.

**E** (equivalent to '$W_2$' in Nadachowski, 1982, 'e' according to Rekovets and Nadachowski, 1995): The width of the middle part of the ACC (T6-T7 triangles, respectively) was calculated from the coordinates of LM4 and LM20 points. Alternatively, it can be measured from the outermost point of BSA4 and that of LSA5.

**B** (equivalent to '$B_1$' in Nadachowski, 1982, 'b' in Van der Meulen, 1973 and Rekovets and Nadachowski, 1995): The width of the neck was calculated from the coordinates of points LM5 and LM19, or interpreted as the distance between BRA3 and LRA4. This measurement is similar, but greater than variable '5' of Nadachowski, 1991, which represents the same distance, but is measured along the longitudinal axis of the molar and not directly between LM5 and LM 19.

**C2** (equivalent to '$C_2$' in Nadachowski, 1982): The length of the middle part of the ACC (T6-T7 triangles, respectively) calculated from the coordinates of LM3 and LM19, or measured from the inflexion point of BRA4 and that of LRA4. '$C_1$' in Nadachowski, 1982 (which is equivalent to 'c' in Van der Meulen, 1973 and Rekovets and Nadachowski, 1995) were not used here, because it would only be useful for comparing *Microtus* (*Microtus*) with *Microtus* (*Terricola*) and *Microtus* (*Allophaiomys*) morphologies, and the latter two were not studied in the present paper.

In addition to the above mentioned measurements, new variables are also used and defined below (Fig. 5):

**A3**: The length of the anterior part of ACC (AC and T6-T7 triangles) on the lingual side of $m_1$, defined as the distance between LM1 and LM19, measured along the longitudinal axis of the molar from the anterior tip of the molar to the most anterior point of LRA4.

**C3**: The length of the posterior part of the ACC (T4-T5 triangles, respectively) calculated from the coordinates of LM5 and LM17 points, or measured from the inflexion point of BRA3 and that of LRA3.

After defining the distances of the specified points in pixels, a scaling factor was used to transform the values into millimetres.

These measurements were used to calculate the following indices: **A/L** = A*100/L, **D/E** = D*100/E (= '$B_2/W_2$' in Nadachowski, 1982), **B/L** = B*100/L, and **C2/E** = C2*100/E. The total number of variables and indices used in the traditional morphometric analyses is 14.

*5.3. Tests for normality and statistical comparisons*

Prior to comparing the different taxa, normality of the distributions was verified by Shapiro-Wilks and Anderson-Darling tests with $\alpha$=0.05. Unimodality was evaluated by Hartigan's dip test with the same significance level. The tests were carried out 500 times on subsamples of 100 randomly selected measurements of each variable for most taxa. If the size of an original sample was lower than 100 specimens (as in the case of *Chionomys nivalis*) then 50 measurements were used for subsampling and the tests were made only 100 times. The values, which fall beyond the lower (the lower quartile (Q1) - 1.5 × the interquartile range (IQR = Q3 − Q1)) and upper whiskers (upper quartile (Q3) + 1.5 × the interquartile range (IQR = Q3 − Q1)) are considered outliers and were excluded from the analysis. The resulting distributions of the p-values were used to assess normality and modality of the

original distributions. If the majority (95%) of the tests rejected the null hypothesis, then normality or unimodality was rejected. A visual inspection of the quantile-quantile plots was used for verification of normality for each variable. In the case of normally distributed data, the points on such plot should fall approximately on a straight line. Lack of fit to the regression line suggest deviations from the normality. An "S"-shaped arrangement of the points, for example, indicates that the sample distribution is either bimodal or has heavier tails than the normal theoretical distribution (Helsel and Hirsch, 2002; Thode, 2002). All calculations were made with the *diptest* and *nortest* packages of R (R Core Team, 2013).

A distribution was considered symmetric if the skewness value calculated by the *moments* package of R (R Core Team, 2013) was between -0.3 and 0.3 and the correlation coefficient of the regression line fitted to the points of the corresponding quantile-quantile plot was higher than 0.98. In order to compare the equality of the mean and variance of the distributions of different taxa both parametric (Welch test and F-test, which are sensitive to non-normality) and non-parametric tests (Kolmogorov-Smirnov test and Kruskal-Wallis test) were used e null hypothesis of equality was rejected if the p-value was lower than 0.05.

*5.4. Clustering and discriminant analysis*

Group structure in the morphometric data was evaluated via two different approaches. The first one, cluster analysis does not assume any a priori classification of observations, and may be used to detect whether any natural grouping exists in the data. Its results may be contrasted with an existing taxonomic classification afterwards to assess how the taxa are reproduced by clustering on the selected variables. The other approach, multiple discriminant analysis (also known as canonical variates analysis) operates the other way round; its input is a classification of observations specified by the investigator. Its objective is to produce an ordination of observations such that separation of these a priori defined groups is maximized

in a space of a few canonical variates. These variates, also called the discriminant functions, are linear combinations of the original variables. The method is useful to quantify how the original variables support the distinction between the groups. For these multivariate analyses, only one variable (L) was chosen from those (L, A, W) that showed high linear correlation ($r > 0.8$) with each other. The correlation coefficient was calculated by the *corrplot* package of R (R Core Team, 2013).

Clustering was performed by the *agnes* package of R (R Core Team, 2013). We used an agglomerative hierarchical algorithm, the average linkage clustering (also called UPGMA = unweighted pair group method using arithmetic averages, Sneath and Sokal, 1973). The analysis employed Euclidean distances calculated between pairs of observations based on the original variables, each standardized to unit variance and zero mean. The results are graphically visualized by a dendrogram. The agglomerative coefficient (AC, Kaufman and Rousseeuw, 1990) was used to assess whether any natural grouping occurs in the data. A high AC value (close to 1.0) indicates that the algorithm has found a natural grouping, whereas a low value (close to 0.0) means that there is no clustering tendency in the data.

Multiple discriminant analysis was performed by the SYN-TAX 2000 multivariate data analysis software (Podani, 2001), following Anderberg (1973). Because the goal is to maximize the between-group dispersion rather than within-group variances on each axis, the spherizing transformation suggested by Mardia et al. (1979) was applied. For visualization, an ordination scatter diagram for the first two most important canonical variates is used. Correlations of the original variables may be projected onto the ordination to yield a biplot diagram which greatly enhances interpretation of results. Isodensity and confidence circles drawn around the centroid of each group may be interpreted statistically, provided that sampling was random and multivariate normality holds.

*5.5. Landmark analysis*

Landmark lysis of LM and SLM points was carried out using the tpsRelw software. According to the software requirements, a links file was prepared to describe the enamel outline and a separate sliders file was made to distinguish landmarks from semi-landmarks with tpsUtil (http://life.bio.sunysb.edu/morph/). The subroutine of *tpsRelw* executes the following steps: in order to eliminate variation in position, size, and orientation, the raw landmark configurations are superimposed on each other using the centroid (i.e. the arithmetic mean of all landmarks) as a ching point. The centred configurations are then scaled to the same centroid size (which represents the square root of the summed squared distances between all landmarks and the centroid) and iteratively rotated until the minimum sum of squared distances between the LM points and their corresponding sample average position is reached. The latter method is known as Generalized Procrustes Analysis (Gower, 1975) and the resulting landmark coordinates are the Procrustes shape coordinates. The residual differences after the Procrustes superimposition can be ascribed to real shape differences or measurement error. The mean shape of the superimposed specimens is the consensus shape. In addition to these transformations, the SLM points are allowed to slide along the outline curve until they match their corresponding sample average positions as closely as possible. This step is justified because the contour line of a molar should be homologous, whereas the individual points do not necessarily satisfy this criterion. Furthermore, because the SLM points do not necessarily represent specific geometric or biological points, their original position is somewhat arbitrary. After these steps, the program executes a relative warp analysis (RWA), which is a principal component analysis (PCA) of Procrustes shape coordinates based on covariance matrix.

The principal component loadings (i.e. the eigenvectors of the covariance matrix of Procrustes shape coordinates) are visualized by deformation grids, and provide information

whether the dominant aspects of shape variation affect the entire structure or are mostly contained in particular parts or regions. ~~A larger eigenvector means larger variance in the position of a given Procrustes shape coordinate~~

The consensus shape of each species was calculated with the method described above. These mean configurations were compared with the consensus shape of the whole sample using Procrustes distance, which was approximated by the Euclidean distance between two sets of Procrustes shape coordinates. The Procrustes distance is a measure of shape difference between two landmark configurations. It is zero only if the configurations have the same shape, and larger than zero otherwise. The Procrustes sum of squares is the sum of squared distances of each landmark of each observation from the consensus position of the same landmark, calculated after the Generalized Procrustes Analysis. This sum of squares may be partitioned into percentage contributions from individual observations, reflecting the relative deviation of each individual from the consensus.

For a detailed discussion of the above mentioned methodology, see Killick (2012), Mitteroecker et al. (2013). Similar analyses were performed on *Microtus* (*Terricola*) molars by Piras et al. (2009, 2010).

## 6. Results

### *6.1. Distribution tests and comparative statistics*

The measurements of the Somssich Hill sample along with basic statistical parameters are summarized in Table 1, those of the Villány 6 and Villány 8 specimens are in Table 2, whereas the modern taxa are treated in Table 3. Almost all of the variables used here are normally distributed, except to three cases. Normality was rejected for the width of the neck (B) in *M. arvalis*, the length of the tooth (L) in *C. nivalis*, and the A/L index in the case of *M. agrestis*. All of the variables have unimodal and more or less symmetric distributions

according to the results of Hartigan's dip tests and the skewness values. These results support the assumption that the voles from the Somssich Hill 2 site referred to the genus *Microtus* (*Microtus*) belong to a single species and do not represent a composite sample of different taxa. They also imply that all of the variables can be used for statistical tests which are sensitive to deviation from normality and symmetry (Welch test and F-test).

In order to confirm that this fossil sample from the Somssich Hill 2 site represents a single species, the variance of the group was compared with three recent species of *Microtus* and *Chionomys nivalis*. The variance of the Somssich Hill sample equals that of one of the recent species in the case of eight variables, two species (*M. arvalis* and *M. agrestis*) in the case of the width of the middle part of the ACC (A2), and three species (*M. arvalis*, *M. agrestis*, and *C. nivalis*) in the case of the length of the anterior part of ACC on the lingual side of a molar (A3). It means that considering the overall variance, the Somssich Hill *Microtus* (*Microtus*) group is remarkably similar to several recent vole species, supporting that the representatives of this fossil assemblage belong to a single species.

In order to exclude the possibility that the Somssich Hill sample represents a mixture of two morphologically close (or almost identical) species, similarly to the recent *M. arvalis* and *M. agrestis*, data from the latter two species were combined and compared as a single group to the other vole samples. The variance of the *M. arvalis-agrestis* group equals to one other species in the case of two variables (A2 and E) and to two species (of which one was the Somssich Hill sample in each case) in the case of two variables (A3 and C2). Therefore, it seems that the overall variance of the Somssich Hill group is more similar to a valid species than the variance of the mixed *M. arvalis-agrestis* group, which means that dividing this fossil assemblage into two different taxa is not justified.

Similar conclusions could be drawn from all tests used here for comparing the means of the distributions. In the case of the Somssich Hill sample, the hypothesis of equality of the

means with the recent species was rejected for almost all of the variables except the width of the neck (B), which was identical to *M. agrestis*, the C2/E index, which was similar to *M. arvalis*, and the A/L index, which was identical to *M. nivalis*. Based on these results, the Somssich Hill *Microtus* (*Microtus*) group represents a statistically distinct taxon considering the means of the studied variables. The recent species are also statistically distinguishable from each other. Even the morphologically similar *M. arvalis* and *M. agrestis* are identical only in the case of the D/E index.

Normality was rejected for two variables (B, C3), and three indices (A/L, D/E and C2/E) in the case of the Villány 8 sample. Unimodality was also rejected for B and C3 variables, but the mentioned three indices were distributed unimodally. These results indicate the presence of more than one species in the Villány 8 *Microtus (Microtus)* material. However, the overall variance of the Villány 8 sample equals with one recent species in the case of three variables (A3 and L – *M. arvalis*; A – *M. oeconomus*), with two species in the case of four variables (C3 and C2/E – *M. oeconomus*, *C. nivalis*; A2 and C2 – *M. agrestis*, *M. oeconomus*), and with three species (*M. agrestis*, *M. oeconomus*, *C. nivalis*) in the case of A/L. The variance also equals with the Somssich Hill and Villány 8 samples in the case of six variables (B, L, D, C2, C2/E and A/L). The fact that the variance tests indicated several similarities with recent species suggests that there is only one *Microtus (Microtus)* species in the Villány 8 sample, which is in contrast with the results of the above described distribution tests.

The means of the distributions were equal with one species in only three cases (A3 – Somssich Hill sample, L – *M. agrestis*, C2/E – *C. nivalis*). This suggest that the Villány 8 sample (representing either one or more species) is considerably distinct from both the Somssich Hill material and the recent species.

Results of the Villány 6 sample are not reliable due to the small sample size. Normality and unimodality of the variables were rejected. Results of the parametric tests (Welch test and

F-test), which are sensitive to non-normality, were not used. On the basis of the Kolmogorov-Smirnov, and Kruskal-Wallis tests, the *Microtus (Microtus)* material from Villány 6 is similar to the Villány 8 sample. Comparing these two localities, the means are equal in the case of four variables (A2, L, D, C2). Some means are also identical to that of recent species (C3, L – *M. agrestis*; A2, C2/E – *C. nivalis*; A – *M. arvalis* and *M. oeconomus*), as well as with the Somssich Hill sample (C2/E).

Only eight specimens were available from Kövesvárad, thus the small sample size precluded any statistical analyses.

*6.2. Cluster and discriminant analyses*

Cluster analysis was used here in order to decide which recent species is the most similar morphologically to the Somssich Hill sample. High agglomerative coefficient (0.8) suggests the presence of a natural grouping in the data. The species involved in the analysis form five distinct groups which make up two larger clusters in the dendrogram, consisting of the (Somssich Hill sample (*M. agrestis*, *M. arvalis*)) and (*M. oeconomus*, *C. nivalis*) (Fig. 6). The larger groups are separated at a distance level of 5.0, whereas all the five species are distinct at approximately 3.0. There is no significant natural separation below the species level. The cluster analysis indicates that the Somssich Hill sample is morphologically close to the recent *M. arvalis-agrestis* group. Despite the morphological similarities, the two species in the latter group formed two closely related, but distinct clusters in the resulting dendrogram. It is notable that *Chionomys nivalis*, a species removed from the genus *Microtus* by several authors (Chaline and Graf, 1988, Nadachowski, 1990b, Bannikova et al., 2010), is not an outgroup, but is placed together with *M. oeconomus* (Fig. 6).

The discriminant function analysis confirmed the above described results of the hierarchical clustering. *M. agrestis*, *M. arvalis* and the Somssich Hill sample are

morphologically close to each other, whereas *M. oeconomus* and *C. nivalis* both take a separate position in the canonical space (Fig. 7).

The main variables responsible for the distinction of the Somssich Hill sample together with the *M. agrestis–M. arvalis* group from the other species are A3, B, C2, D and L, and the indices A/L, C2/E and D/E (Fig. 7). These two groups hardly ever overlap when considering these variables. Because variables C2 and D express the distance between fourth or the fifth lingual re-entrant angles (LRA4 and LRA5, respectively) and the fourth buccal re-entrant angle (BRA4, i.e. the buccal infolding of the cap region), which is missing or undeveloped in the case of the *M. oeconomus–C. nivalis* morphogroup, it is obvious that these variables are longer in the latter species. Variable B is related to the width of the neck (i.e. the distance between the LRA4 and BRA3). Since LRA4 is more anteriorly positioned in the *M. oeconomus–C. nivalis* morphogroup, the neck is more open than in the case of the other three species (Fig. 7). Due to the same morphological change, the distance between LRA4 and most anterior point of the cap reduces, thus variable A3 becomes shorter. The Somssich Hill sample occupies an intermediate position between the *M. oeconomus–C. nivalis* morphogroup and the voles belonging to the *M. agrestis–M. arvalis* group with narrow neck and high A3 values. The two morphogroups also differ in size, teeth that belong to the *M. oeconomus–C. nivalis* morphogroup being longer (thus having higher L values).

None of the studied variables allow clear separation of *M. agrestis* from *M. arvalis* within the group that also contains the Somssich Hill sample (Fig. 7). The Somssich Hill sample can only be separated from the *M. agrestis–M. arvalis* group on the basis of one variable (A3) and two indices (A/L, D/E). It means that the recent species have a slightly longer cap region (A, A3). In addition, the distance between BRA4 and LRA5 (D) reduces (i.e. the anterior infolding of the cap becomes more emphasized).

The differences in the other morphogroup between *M. oeconomus* and *C. nivalis* are more obvious (Fig. 7). There are no overlaps between these species in the case of four variables (A2, A3, C3, E). The teeth of *M. oeconomus* are narrower (which results smaller E values), but their cap regions are longer (i.e. they have higher A2 and A3 values).

It seems that *Chionomys* as a representative of a different lineage can most effectively be separated from voles belonging to the genus *Microtus* based on the length of the posterior part of the anteroconid-complex (C3). These genera hardly ever overlap regarding this variable (Fig. 8). The C3 of *Chionomys* is typically higher than 0.4 mm (mean = 0.47 ± 0.04 mm), whereas that of *Microtus* is usually below 0.4 mm (mean = 0.29 ± 0.08 mm). In the Somssich Hill sample, all C3 values are below 0.4 mm (mean = 0.29 ± 0.04 mm), which means that all specimens in this sample can be referred to the genus *Microtus*.

In the dendrogram produced by the cluster analysis of the Villány 6 and Villány 8 samples and the recent species, four distinct groups are present which belong to two major clusters: (((Villány 8 sample, Villány 6 sample) (*C. nivalis*)) (*M. oeconomus*))) and (*M. arvalis*, *M. agrestis*) (Fig. 9). The larger groups are separated at a distance of 22.0, whereas all the three smaller clusters are distinct at approximately 16.0. The results suggest that the Villány 6 and Villány 8 samples are morphologically very close to each other, similarly to the recent *M. arvalis-agrestis* group. These fossil species are most similar to *C. nivalis* among the recent voles, but the Villány 8 sample is morphologically similar to *M. oeconomus* as well.

The discriminant analysis that was based on the material from Villány 6 and Villány 8 and the recent taxa confirmed the results of the clustering. These fossil samples are morphologically close to *C. nivalis* and *M. oeconomus*, but they are clearly distinct from the *M. agrestis–M. arvalis* group (Fig. 10a). Based on the C3 values that are lower than 0.4 mm (Villány 8 mean = 0.28 ± 0.07 mm; Villány 6 mean = 0.34 ± 0.06 mm), these fossil samples can be referred to the genus *Microtus* rather than *Chionomys*.

The cluster analysis of all of the the fossil samples showed that a large part of the Somssich Hill sample forms a separate group together with the Kövesvárad material, but some specimens are morphologically closer to the Villány 6 and Villány 8 samples (overlapping forms on Fig. 11).

The discriminant analysis of the fossil samples showed that the specimens from Kövesvárad can be separated from the Somssich Hill sample on the basis of variables A3 and C3 only. The main variables responsible for the distinction of the Somssich Hill sample and the Villány 6 – Villány 8 group are variables A2, C2, D, E and L (Fig. 10b). Variables C2 and D express the distance between the fourth or the fifth lingual re-entrant angles (LRA4 and LRA5, respectively) and the fourth buccal re-entrant angle (BRA4). Because both the buccal (BRA4) and the lingual (LRA5) infoldings at the cap region are underdeveloped in the case of the Villány 6 – Villány 8 group, it is obvious that these variables are longer in the latter samples. BRA3 is also slightly underdeveloped in the case of the Villány 8 sample (but not in the Villány 6 sample). As a consequence, the distance between this region and the most anterior point of the cap (A2) increases compared to the Somssich Hill sample. Variable E represents the distance between BSA4 and LSA5. Because LSA5 is more anteriorly positioned in the case of the Villány 6 – Villány 8 group, higher E values can be measured on the latter teeth (Fig. 10b). In addition the teeth are longer, thus they have higher L values in the Villány 6 – Villány 8 group.

*6.3. Landmark and Procrustes analyses*

Landmark analysis was used in order to find the consensus shape in the Somssich Hill sample and to reveal and visualize the shape variance of the occlusal surface within the studied fossil and recent vole species. The first two axes of the relative warp analysis of the landmark points explain 51% of the overall variance. The drop in the variance explained by

each consecutive axis is slight to moderate, however, more than 70% of total variance is explained by the first 6 axes. Each species forms distinct groups along the first two ordination axes, except *M. agrestis* and *M. arvalis*, which occupy almost the same location in the morphospace. The Somssich Hill sample is located centrally in the morphospace, whereas the other species have marginal positions (Fig. 12a). Regarding the shape of the occlusal surface, all possible morphological transitions towards the studied recent species exist within the Somssich Hill sample. It means that the morphologies located on the edge of the Somssich Hill sample point cloud are hardly separable from the individuals belonging to other species which are located adjacent to them (Fig. 13).

Eigenvectors of each landmark points were used in order to reveal the most important shape changes associated with the principal components. The ten largest vectors belonged to the nine landmark points on the cap (LM1-5 and LM19-22) and the most posterior point of the tooth (LM11). It means that the differences in the cap shape are the main factors behind the distinction of the groups, whereas the posterior part of the molars shows a conservative morphology, apart from the overall length.

In order to quantify the observed morphometric differences between the analysed species, the consensus shapes of each species were compared to a hypothetical shape calculated from the consensus coordinates of all of the five studied taxa. From the percentage contributions to the total sum of squares found that the Somssich Hill sample is the most similar to the hypothetical average shape (3.8%). *M. agrestis* and *M. arvalis* differ from the average approximately to a similar extent (12.7% and 17.1%, respectively). *M. oeconomus* and *C. nivalis* represent the most distinct morphologies, with percentage contributions to deviation from the mean shape of 32.3% and 34.0%, respectively.

Although the point clouds of the Villány 6 and Villány 8 samples partially overlap with the Somssich Hill sample, they are clearly distinguishable from it, and located in the

morphospace between the point clouds of *M. oeconomus* and *C. nivalis*, partially overlapping with *C. nivalis*. On the other hand, the Kövesvárad sample cannot be separated from the Somssich Hill material on the basis of the landmark analysis (Fig. 12b).

## 7. Discussion

### *7.1. Taxonomy*

Four different *Microtus* species were reported from West Runton (Norfolk, Great Britain), a site of comparable age (early Middle Pleistocene, MIS 19-17) with the Somssich Hill 2 and Villány 6 and Villány 8 localities: *M. arvalinus*, *M. nivalinus*, *M. nivaloides* and *M. ratticepoides* (Hinton, 1923; Forsyth Major, 1902). According to the revision of Nadachowski (1990b), *M. arvalinus* is a junior synonim of *M. nivaloides*, whereas *M. ratticepoides* is a junior synonim of *M. nivalinus.*

Although Jánossy (1990, 1999) assigned the 'true' *Microtus* material from the Somssich Hill 2 site to four different species, our above described results suggest that it should rather be referred to a single species. Van der Meulen (1973) mentioned two distinct *Microtus* (*Microtus*) species from Villány 6 and Villány 8, which was also rejected by our analyses. We think that the Somssich Hill sample and the Villány 6 – Villány 8 morphogroup represent most likely two distinct species. Considering the morphological similarities, we argue that the material from the Somssich Hill 2 locality is best referred to *M. nivaloides*, whereas the Villány 6 and Villány 8 samples should be assigned to *M. nivalinus*.

#### 7.1.1. *Microtus (Microtus) nivaloides* from the Somssich Hill 2 locality

Based on 587 specimens, our study revealed that *Microtus nivaloides* was a small-sized *Microtus (Microtus)* species with plesiomorph characters and basal cap morphology somewhat similar to *Microtus (Allophaiomys)*. Shallow, nearly equally-sized re-entrant angles

(LRA5, BRA4) appear on both sides of the cap. This feature establishes similarity to the *M. arvalis-agrestis* group, but not to *Chionomys nivalis* and *M. oeconomus* (Fig. 14). The strong, anteriorly directed infolding of LRA4 and the relatively large distance between LRA4 and BRA3 (i.e. the open neck) are similar to *C. nivalis* and *M. oeconomus*. These features clearly separate the *M. nivaloides* morphology from the recent *M. arvalis-agrestis* group with an inward pointed LRA4 and a narrow neck.

7.1.2. *Microtus (Microtus) nivaloides* from the Kövesvárad locality

Because of the small sample number (eight specimens), the Kövesvárad sample (which is slightly younger than the Somssich Hill sample) was not suitable for statistical analyses, but nevertheless was included in the geometric morphometric study leading to taxonomically meaningful results. The morphology of the teeth is more similar to the material from the Somssich Hill site than to the teeth from the Villány 6 and Villány 8 localities, thus we referred these molars to *M. nivaloides*.

7.1.3. *Microtus (Microtus) nivalinus* from the Villány 6 and Villány 8 localities

Because the Villány 6 and Villány 8 localities are slightly younger than the Somssich Hill 2 site, our stratigraphic data suggest that *Microtus nivalinus* appeared somewhat later than *M. nivaloides* in the area. Although all *Microtus* (*Microtus*) specimens from both Villány 6 and Villány 8 sites are thought to belong to *M. nivalinus*, they display slight morphological differences. Based on a comparison of the consensus shapes, a gradual morphological transition could be detected between *M. nivaloides* from Somssich Hill 2 and *M. nivalinus* from Villány 8, in which the morphology of the specimens from Villány 6 represent an intermediate state (Fig. 14).

Compared to *M. nivalinus* from Villány 8, the infolding of the cap is more prominent (i.e. the D values are lower) in the case of the teeth from the Villány 6 site. BRA4 and LRA5 are more prominent in *M. nivaloides* from Somssich Hill 2, therefore their D value is even lower. The width of the neck is approximately the same in *M. nivaloides* from Somssich Hill 2 and *M. nivalinus* from Villány 6, but the neck is more open (i.e. the B values are higher) in the Villány 8 sample. The cap morphology of the Villány 8 specimens are slightly similar to the recent *M. oeconomus*. The neck is open, BRA4 is present but not well-developed, and BSA4 is clearly distinguishable. The cap is slightly flattened (similarly to the Villány 6 sample and the recent *C. nivalis*) but not rounded as in the case of *M. nivaloides* and the recent *M. oeconomus*. The cap region of specimens in the Villány 6 and Villány 8 samples is slightly mesiobuccally rotated compared to *M. nivaloides* (Fig. 14).

7.2. Evolutionary and ecological interpretation

With its age of approximately 1.0–0.9 Ma, the late Early Pleistocene material of the Somssich Hill 2 site represents one of the earliest occurrences of *M. nivaloides* in Central Europe. Geographically and temporally it provides an important record of the initiation of radiation of 'true' *Microtus* species which most likely led to the present diversity of this group (Rabeder, 1981). Our analyses suggest that *M. nivaloides* have a morphology which is centrally positioned in a morphospace defined on the basis of the extant *Microtus* (*Microtus*) species in the region. The morphology of its occlusal surface shows transitional features towards all of the recent taxa included in this study, which suggests that *M. nivaloides* is the likely ancestor from which the recent *Microtus (Microtus)* species evolved. The material from Villány 6 and Villány 8 indicates that approximately 200 kyr later, an additional 'true' *Microtus* species, *M. nivalinus* appeared in the region, but the contemporaneous material from Kövesvárad suggests that *M. nivaloides* was still present. Morphological similarity between

the material from the Somssich Hill 2 site and the recent *M. arvalis-agrestis* group suggests that both *M. arvalis* and *M. agrestis* evolved from *M. nivaloides*, whereas *M. nivalinus* belongs to the lineage which led to *M. oeconomus* (Fig. 15). Rabeder (1981) suggested that *M. oeconomus* evolved from *Microtus (Terricola) hintoni* instead of *M. nivalinus*. The latter species led to the emergence of *Chionomys nivalis* in his model. However, our evolutionary model agrees with that of Nadachowski (1991) and Maul and Markova (2007) regarding the evolution of the above mentioned lineages.

The ecological needs of *M. nivaloides* and *M. nivalinus* are best inferred from the ecological preferences of the other taxa in the accompanying fauna. According to Jánossy (1986), the dominant species of the Kövesvárad site (*Glis sackdillingensis*, *Muscardinus dacicus*, *Apodemus sylvaticus*, *Myodes* sp.) likely lived in a forested environment. However, a few other, albeit more rare taxa (e.g. *Allocricetus bursae*, *Cricetus praeglacialis* and *Ochotona* sp.) suggest a more open vegetation. The contemporaneous assemblages of Villány 6 and Villány 8 sites are remarkably different from those at Kövesvárad, which are dominated by species adapted to an open, steppe environment (*Allocricetus bursae*, *Cricetus praeglacialis*, *Prolagurus pannonicus, Crocidura obtusa*). The Villány Mountains (southern Hungary) and the Bükk Mountains (Kövesvárad, northeastern Hungary) therefore appear to represent different environments with different vegetation in the early Middle Pleistocene. The degree of their dissimilarity resembles the present conditions. In addition, it seems that *M. nivalinus* preferred open habitats, whereas *M. nivaloides* was restricted to forested areas. The fauna of the slightly older Somssich Hill 2 site allows similar paleoecological inferences. *M. nivaloides* is markedly less abundant in layers with dominant species indicative of steppe environment (e.g. *Allocricetus bursae*, *Cricetus runtonensis*, *Lagurodon arankae*, *Prolagurus pannonicus*).

## 8. Conclusions

A combination of distribution analyses, clustering and discriminant analyses of standa morphometric measurements, and relative warp analysis of landmark data was suc fully used in the case of c. 800 fossil and 1500 recent vole lower first molars belonging to the genera *Microtus* (*Microtus*) and *Chionomys*.

We developed a method distinguish vole specimens of the genus *Chionomys* from *Microtus*. The length of the posterior part of the anteroconid-complex (C3) is typically larger than 0.4 mm for *Chionomys*, whereas it remains below 0.4 mm for *Microtus* specimens. Based on the C3 values, all of the fossil material studied here is referred to the genus *Microtus*.

~~Almost all of the variables used here are unimodally and nearly symmetrically distributed in both the fossil sample from Somssich Hill 2 and the recent material used for comparison.~~ The variance of the Somssich Hill 2 sample is more similar to that in any single recent valid species included in the analysis than to the variance of the mixed *M. arvalis-agrestis* group. These observations suggest that the fossil material should be referred to a single species and do not represents a composite sample which contains different taxa. In addition, the cluster analysis indicates that the Somssich Hill sample is morphologically close to the recent *M. arvalis-agrestis* group.

The Villány 6 and Villány 8 samples are morphologically close to each other (to a degree comparable to the similarity within the recent *M. arvalis-agrestis* group), but they are clearly distinct from both the Somssich Hill material and the recent species. These fossil species are most similar to *C. nivalis* among the recent voles, but the Villány 8 sample is morphologically similar to *M. oeconomus* as well.

Morphological similarities suggest that the material from the Somssich Hill 2 locality should be referred to *M. nivaloides*, whereas the Villány 6 and Villány 8 samples should be

assigned to *M. nivalinus*. Here we provide detailed diagnoses for these species, on the basis of the consensus shapes of each taxa and the mathematical statistical assessment of the whole sample.

Known ecological preferences of other taxa in the accompanying fauna allow to infer that *M. nivalinus* preferred open habitats, whereas *M. nivaloides* was restricted to forested areas. The observed morphological similarities with the studied recent taxa suggest that both *M. arvalis* and *M. agrestis* evolved from *M. nivaloides*, whereas *M. nivalinus* belongs to another lineage which led to *M. oeconomus*. However, a more complete stratigraphical record would be necessary to fully clarify the phylogenetic relationships of the recent taxa, and to track the morphological changes at high temporal resolution between the late Early Pleistocene and the appearance of the extant species.

**Acknowledgements**

The authors are grateful for F. James Rohlf (Stony Brook University, New York, USA) and Ádám Kocsis for their help with the softwares used in the paper. Thanks are due to Gábor Csorba, Tamás Görföl and Mihály Gasparik for providing access to the collections in their care at the Hungarian Natural History Museum. We are indebted to the colleagues at the Dept. of Paleontology and Geology at the HNHM, as well as the Dept. of Paleontology and the Dept. of Physical and Applied Geology at the ELTE for their support throughout this project. Mariann Bosnakoff, Emese Németh and Anna Zsolt are thanked for technical assistance. This study was sponsored by the Hungarian Scientific Research Fund (OTKA K104506). Help by the other members of this OTKA project and the field crew of the excavations at the Somssich Hill 2 site is also acknowledged. This paper is MTA-MTM-ELTE Paleo contribution No. 236.

**References**

Anderberg, M.R., 1973. Cluster Analysis for Applications. Academic Press, New York.

Antoñanzas, R.L., Cuenca Bescós, G., 2002. The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals. Palaeogeography, Palaeoclimatology, Palaeoecology 186, 311–334.

Bannikova A.A., Lebedev V.S., Lissovsky A.A., Matrosova V., Abramson N.I., Obolenskaya E.V., Tesakov A.S., 2010. Molecular phylogeny and evolution of the Asian lineage of vole genus *Microtus* (Rodentia: Arvicolinae) inferred from mitochondrial cytochrome *b* sequence. Biological Journal of the Linnean Society 99, 595–613.

Botka, D., Mészáros, L., 2014. *Beremendia* (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (Southern Hungary) and their taxonomic, biostratigraphic, palaeoecological and palaeobiogeographical relations. Fragmenta Palaeontologica Hungarica 31, 79–111.

Chaline, J., Graf, J.-D., 1988. Phylogeny of the Arvicolidae (Rodentia): biochemical and paleontological evidence. Journal of Mammalogy 69, 22–33.

Fejfar, O., Heinrich, W.-D., Lindsay, E.H., 1998. Updating the Neogene Rodent biochronology in Europe. The Dawn of the Quaternary, Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60, 533–553.

Forsyth Major, C.I., 1902. On some jaws and teeth of Pliocene Voles (*Mimomys*, gen. nov.), from the Norwich Crag at Thorpe, and from the Upper Val d'Arno. Proceedings of the Zoological Society of London, February 18, 1902, 102–107.

Gower, J.C., 1975. Generalized Procrustes analysis. Psychometrika 40, 33–51.

Helsel D.R., Hirsch R.M., 2002. Statistical Methods in Water Resources. USGS Techniques of Water Resources Investigations, Book 4, Chapter A3.

Hillson, S., 2005. Teeth. Cambridge Manuals in Archaeology, Cambridge University Press, Cambridge.

Hinton, M.A.C., 1923. Diagnoses of species of *Pitymys* and *Microtus* occurring in the Upper Freshwater Bed of West Runton, Norfolk. Annals and Magazine of Natural History 9(12), 541–542.

Hír, J., 1998. Cricetids (Rodentia, Mammalia) of the Early Pleistocene vertebrate fauna of Somssich-hegy 2 (Southern Hungary, Villány Mountains). Annales Historico-Naturales Musei Nationalis Hungarici 90, 57–89.

Jánossy, D., 1963. Die altpleistozäne Wirbeltierfauna von Kövesvárad bei Répáshuta (Bükk-Gebirge). Annales historico-naturales Musei nationalis hungarici 55, 109–141.

Jánossy, D., 1983. Lemming-remain from the Older Pleistocene of Southern Hungary (Villány, Somssich-hegy 2). Fragmenta Mineralogica et Palaeontologica 11, 55–60.

Jánossy, D., 1986. Pleistocene vertebrate faunas of Hungary. Akadémiai Kiadó, Budapest.

Jánossy, D., 1990. Arvicolids from the Lower Pleistocene sites at Beremend 15 and Somssich-hegy 2, Hungary. In: Fejfar, O., Heinrich, W.-D. (Eds.), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia), Geological Survey, Prague, pp. 223–230.

Jánossy, D., 1999. Additional data to the fossil material of the Somssich Hill 2 site (Villány Mts.). Manuscript (in Hungarian), Department of Paleontology and Geology, Hungarian Natural History Museum, Budapest, Hungary.

Kaufman, L., Rousseeuw P.J., 1990. Finding Groups in Data: An Introduction to Cluster Analysis. Wiley Series in Probability and Mathematical Statistics. Applied Probability and Statistics. Wiley, New York.

Killick, L.E., 2012. Geometric morphometric analysis of the *Microtus* $M_1$ and its application to Early Middle Pleistocene in the UK. Ph.D. thesis, Durham University, UK.

Kolfschoten van T., Markova A.K., 2005. Response of the European mammalian fauna to the mid-Pleistocene transition. In: Head, M.J., Gibbard, P.L. (Eds.), Early-Middle Pleistocene Transitions: The Land-Ocean Evidence. Geological Society, London, Special Publications 247, 221–229.

Kordos, L., 1994. Revised Biostratigraphy of the Early Man Site at Vértesszölös, Hungary. Courier Forschungs-Institut Senckenberg 171, 225–236.

Kretzoi, M., 1956. A Villányi hegység alsó-pleisztocén gerinces-faunái (Die Altpleistozänen wirbeltierfaunen des Villányer Gebirges). Geologica Hungarica series Palaeontologica 27, 1–264.

Kretzoi, M., Pécsi, M., 1982. Pliocene and Quaternary chronostratigraphy and continental surface development of the Pannonian Basin. In: Pécsi M. (Ed.), Quaternary studies in Hungary, Geographical Research Institute Hungarian Academy of Sciences, Budapest, pp. 11–42.

Mardia, K.V., Kent, J.T., Bibby, J.M., 1979. Multivariate Analysis. Academic Press, London.

Maul, L.C., Markova, A.K., 2007. Similarity and regional differences in Quaternary arvicolid evolution in Central and Eastern Europe. Quaternary International 160, 81–99.

Maul, L.C., Parfitt, S.A., 2010. Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. Quaternary International 228(1–2), 91–115.

Maul, L.C., Masini, F., Parfitt, S.A., Rekovets, L., Savorelli, A., 2013. Evolutionary trends in arvicolids and the endemic murid *Mikrotia* – New data and a critical overview. Quaternary Science Reviews 96, 240–258.

Mayhew, D.F., 2009. The type material and the enamel structure of *Villanyia exilis* KRETZOI, 1956 (Arvicolidae, Rodentia). Acta Zoologica Cracoviensia 52A(1–2), 81–94.

Meulen, van der A.J., 1973. Middle Pleistocene smaller mammals from the Monte Peglia, (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). Quaternaria 17, 1–144.

Mitteroecker, P., Gunz, P., Windhager, S., Schaefer, K., 2013. A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. Hystrix, the Italian Journal of Mammalogy 24(1), 59–66.

Nadachowski, A., 1982. Late Quaternary rodents of Poland with special reference to morphotype dentition analysis of voles. Państwowe Wydawnictwo Naukowe, Warszawa–Kraków.

Nadachowski, A., 1985. Biharian voles (Arvicolidae, Rodentia, Mammalia) from Kozi Grzbiet (Central Poland). Acta Zoologica Cracoviensia 29(2), 13–28.

Nadachowski, A., 1990a. Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. Quartärpaläontologie 8, 215–223.

Nadachowski, A., 1990b. Comments on variation, evolution and phylogeny of Chionomys (Arvicolidae). In: Fejfar, O., Heinrich, W.-D. (Eds.), International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Geological Survey, Prague, pp. 353–368.

Nadachowski, A., 1991. Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. Acta Theriologica 36(1-2), 1–45.

Pazonyi, P., Mészáros, L., Szentesi, Z., Gasparik, M., Virág, A., 2013. Preliminary Results of the Palaeontological Investigations of the Late Early Pleistocene Somssich Hill 2 Locality (South Hungary). 14th Congress of Regional Committee on Mediterranean Neogene Stratigraphy, Book of Abstracts of the RCMNS 2013, Istanbul Technical University, Istanbul, p. 270.

Petruso, D., Locatelli, E., Surdi, G., Valle, C.D., Masini, F., Sala, B., 2011. Phylogeny and biogeography of fossil and extant *Microtus* (*Terricola*) (Mammalia, Rodentia) of Sicily and the southern Italian peninsula based on current dentalmorphological data. Quaternary International 243, 192–203.

Piras, P., Marcolini, F., Raia, P., Curcio, M.T., Kotsakis, T., 2009. Testing evolutionary stasis and trends in first lower molar shape of extinct Italian populations of *Terricola savii* (Arvicolidae, Rodentia) by means of geometric morphometrics. Journal of Evolutionary Biology 22(1), 179–91.

Piras, P., Marcolini, F., Raia, P., Curcio, M.T., Kotsakis, T., 2010. Ecophenotypic variation and phylogenetic inheritance in first lower molar shape of extant Italian populations of *Microtus* (*Terricola*) *savii* (Rodentia). Biological Journal of the Linnean Society 99(3), 632–647.

Podani, J., 2001. SYN-TAX 2000. Computer programs for data analysis in ecology and systematics. User's Manual. Scientia, Budapest.

Popov, V.V., Marinska, M., 2007. An almost one million year long (Early to Late Plaistocene) small mammal succession from the archaeological layers of Kozarnika Cave in Northern Bulgaria. Courier Forschungs-Institut Senckenberg 259, 79–92.

Rabeder, G., 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beiträge zur Paläontologie Österreichs 8, 1–373.

Rekovets, L., Nadachowski, A., 1995. Pleistocene voles (Arvicolidae) of the Ukraine. Paleontologia i Evolucio 28–29, 145–245.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Sneath, P.H.A., Sokal, R.R., 1973. Numerical Taxonomy: The Principles and Practice of Numerical Classification. Freeman, San Francisco.

Striczky, L., Pazonyi, P., 2014. Taxonomic study of the dormice (Gliridae, Mammalia) fauna from the late Early Pleistocene Somssich Hill 2 locality (Villány Mountains, South Hungary) and its palaeoecological implications. Fragmenta Palaeontologica Hungarica 31, 49–78.

Szentesi, Z., 2014. Előzetes eredmények a késő kora-pleisztocén Somssich-hegy 2 (Villányi-hegység) ősgerinces-lelőhely kétéltűinek vizsgálatában (Preliminary results on a study of amphibians of the late Early Pleistocene Somssich Hill 2 palaeovertebrate locality (Villány Mountains)). Földtani Közlöny 144(2), 165–174 (in Hungarian with English abstract).

Szentesi, Z., 2016. Urodeles from the Lower Pleistocene Somssich Hill 2 palaeovertebrate locality (Villány Hills, Hungary). Földtani Közlöny 146(1), 37–46.

Thode HC., 2002. Testing for Normality. CRC Press, Cleveland.

http://life.bio.sunysb.edu/morph/

## Tables

Table 1. Basic statistical parameters of the morphometric measurements of *Microtus nivaloides* from Somssich Hill 2 site.

| ***Microtus nivaloides* – Somssich Hill 2 (n=587)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.05 | 1.31 | 1.71 | 0.10 |
| **A2** | 0.54 | 0.77 | 1.02 | 0.08 |
| **A3** | 0.36 | 0.59 | 0.85 | 0.09 |
| **C2** | 0.05 | 0.28 | 0.50 | 0.06 |
| **C3** | 0.09 | 0.30 | 0.46 | 0.06 |
| **D** | 0.19 | 0.42 | 0.62 | 0.07 |
| **E** | 0.57 | 0.75 | 1.00 | 0.06 |
| **L** | 2.15 | 2.60 | 3.27 | 0.17 |
| **B** | 0.05 | 0.20 | 0.44 | 0.07 |
| **W** | 0.74 | 0.93 | 1.15 | 0.07 |
| **A/L** | 45.09 | 50.13 | 54.50 | 1.72 |
| **C2/E** | 8.23 | 37.83 | 70.20 | 9.64 |
| **D/E** | 26.03 | 56.96 | 86.22 | 10.03 |
| **B/L** | 1.71 | 7.57 | 16.41 | 2.81 |

Table 2. Basic statistical parameters of the morphometric measurements of *Microtus nivalinus* from localities Villány 6 and Villány 8.

| ***Microtus nivalinus* – Villány 6 (n=26)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.09 | 1.28 | 1.55 | 0.10 |
| **A2** | 0.57 | 0.73 | 0.89 | 0.08 |
| **A3** | 0.38 | 0.55 | 0.63 | 0.06 |
| **C2** | 0.24 | 0.31 | 0.39 | 0.04 |
| **C3** | 0.18 | 0.32 | 0.43 | 0.06 |
| **D** | 0.36 | 0.50 | 0.61 | 0.06 |
| **E** | 0.66 | 0.77 | 0.86 | 0.05 |
| **L** | 2.34 | 2.64 | 3.04 | 0.14 |
| **B** | 0.09 | 0.20 | 0.34 | 0.06 |
| **W** | 0.91 | 0.97 | 1.01 | 0.03 |
| **A/L** | 45.03 | 48.52 | 52.22 | 1.86 |
| **C2/E** | 29.91 | 40.43 | 52.01 | 6.29 |
| **D/E** | 45.75 | 64.94 | 80.75 | 8.48 |
| **B/L** | 3.61 | 7.72 | 12.31 | 2.25 |

| ***Microtus nivalinus* – Villány 8 (n=178)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.02 | 1.33 | 1.63 | 0.11 |
| **A2** | 0.58 | 0.80 | 1.00 | 0.09 |
| **A3** | 0.37 | 0.54 | 0.78 | 0.08 |
| **C2** | 0.20 | 0.35 | 0.57 | 0.06 |
| **C3** | 0.09 | 0.27 | 0.58 | 0.07 |
| **D** | 0.36 | 0.56 | 0.75 | 0.08 |
| **E** | 0.49 | 0.79 | 1.02 | 0.09 |
| **L** | 2.13 | 2.83 | 3.49 | 0.21 |
| **B** | 0.07 | 0.31 | 0.47 | 0.07 |
| **W** | 0.77 | 1.05 | 1.26 | 0.09 |
| **A/L** | 41.69 | 47.04 | 52.83 | 1.71 |
| **C2/E** | 22.78 | 45.16 | 77.18 | 9.03 |
| **D/E** | 47.67 | 71.45 | 94.88 | 7.88 |
| **B/L** | 2.38 | 11.07 | 16.31 | 2.44 |

Table 3. Basic statistical parameters of the morphometric measurements of the recent taxa (*Microtus agrestis, M. arvalis, M. oeconomus* and *Chionomys nivalis*).

| ***Microtus agrestis* – recent (n=354)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.32 | 1.57 | 1.86 | 0.11 |
| **A2** | 0.80 | 0.97 | 1.21 | 0.08 |
| **A3** | 0.55 | 0.80 | 1.08 | 0.09 |
| **C2** | 0.06 | 0.28 | 0.49 | 0.07 |
| **C3** | 0.09 | 0.36 | 0.51 | 0.05 |
| **D** | 0.14 | 0.33 | 0.54 | 0.06 |
| **E** | 0.70 | 0.87 | 1.04 | 0.05 |
| **L** | 2.49 | 2.90 | 3.36 | 0.18 |
| **B** | 0.05 | 0.17 | 0.43 | 0.06 |
| **W** | 0.86 | 1.06 | 1.29 | 0.06 |
| **A/L** | 47.82 | 54.17 | 59.62 | 1.52 |
| **C2/E** | 6.32 | 32.79 | 69.33 | 8.94 |
| **D/E** | 16.06 | 37.62 | 68.87 | 7.20 |
| **B/L** | 1.81 | 5.84 | 14.93 | 2.07 |

| ***Microtus oeconomus* – recent (n=444)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.07 | 1.38 | 1.80 | 0.09 |
| **A2** | 0.56 | 0.88 | 1.21 | 0.10 |
| **A3** | 0.40 | 0.56 | 0.77 | 0.06 |
| **C2** | 0.27 | 0.45 | 0.62 | 0.06 |
| **C3** | 0.05 | 0.22 | 0.50 | 0.08 |
| **D** | 0.33 | 0.50 | 0.67 | 0.05 |
| **E** | 0.52 | 0.73 | 0.88 | 0.05 |
| **L** | 2.32 | 2.79 | 3.30 | 0.14 |
| **B** | 0.15 | 0.36 | 0.60 | 0.08 |
| **W** | 0.83 | 1.04 | 1.19 | 0.05 |
| **A/L** | 45.62 | 49.52 | 57.01 | 1.59 |
| **C2/E** | 35.16 | 62.41 | 90.02 | 8.28 |
| **D/E** | 47.44 | 68.47 | 106.97 | 6.79 |
| **B/L** | 5.04 | 12.80 | 20.44 | 2.76 |

| ***Microtus arvalis* – recent (n=628)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.11 | 1.39 | 1.70 | 0.11 |
| **A2** | 0.68 | 0.89 | 1.14 | 0.08 |
| **A3** | 0.52 | 0.77 | 1.02 | 0.08 |
| **C2** | 0.11 | 0.28 | 0.40 | 0.05 |
| **C3** | 0.11 | 0.29 | 0.42 | 0.04 |
| **D** | 0.05 | 0.28 | 0.51 | 0.06 |
| **E** | 0.62 | 0.76 | 0.92 | 0.05 |
| **L** | 2.16 | 2.54 | 3.04 | 0.17 |
| **B** | 0.04 | 0.12 | 0.28 | 0.04 |
| **W** | 0.77 | 0.90 | 1.12 | 0.06 |
| **A/L** | 49.30 | 54.83 | 61.76 | 1.42 |
| **C2/E** | 12.51 | 37.01 | 57.64 | 6.61 |
| **D/E** | 6.06 | 36.77 | 70.20 | 7.97 |
| **B/L** | 1.73 | 4.88 | 10.54 | 1.57 |

| ***Chionomys nivalis* – recent (n=96)** | | | | |
|---|---|---|---|---|
| | **min** | **mean** | **max** | **sd** |
| **A** | 1.27 | 1.52 | 1.75 | 0.10 |
| **A2** | 0.61 | 0.78 | 1.03 | 0.08 |
| **A3** | 0.31 | 0.54 | 0.75 | 0.09 |
| **C2** | 0.21 | 0.39 | 0.55 | 0.08 |
| **C3** | 0.14 | 0.46 | 0.70 | 0.09 |
| **D** | 0.25 | 0.69 | 0.93 | 0.12 |
| **E** | 0.62 | 0.89 | 1.05 | 0.09 |
| **L** | 2.46 | 3.04 | 3.38 | 0.16 |
| **B** | 0.09 | 0.25 | 0.43 | 0.08 |
| **W** | 0.89 | 1.14 | 1.26 | 0.07 |
| **A/L** | 45.32 | 49.96 | 54.86 | 1.73 |
| **C2/E** | 27.49 | 44.00 | 63.58 | 8.65 |
| **D/E** | 40.68 | 76.89 | 100.54 | 11.63 |
| **B/L** | 2.77 | 8.25 | 14.83 | 2.56 |

**Figure captions**

Fig. 1. Map of Villány (southern Hungary) and Kövesvárad (northeastern Hungary) with the enlargement of the three sites near Villány. Abbreviations: 2: Somssich Hill 2; 6: Villány 6; 8: Villány 8.

Fig. 2. Stratigraphic position of the studied vertebrate sites and their comparison with other European localities mentioned in the text (biochronological framework after Kretzoi and Pécsi, 1982; Fejfar et al., 1998; Maul et al., 2013). Evolution of *Microtus* are shown after Maul and Parfitt (2010).

Fig. 3. Terminology used for the description of first lower molars of voles.

Fig. 4. Position of landmark and semi-landmark points used in this study on the first lower molars of voles.

Fig. 5. Morphometric measurements used in this study on the first lower molars of voles.

Fig. 6. Dendrogram produced by hierarchical clustering of morphometric data on first lower molars of four recent vole species and fossil material from the Somssich Hill 2 site.

Fig. 7. Biplots produced by discriminant analysis of morphometric data on first lower molars of four recent vole species and fossil material from the Somssich Hill 2 site.

Fig. 8. Box-and-whisker plots of C3 measurements on specimens belonging to the genera *Microtus* and *Chionomys*.

Fig. 9. Dendrogram produced by hierarchical clustering of morphometric data on first lower molars of four recent vole species and fossil material from sites Villány 6 and Villány 8.

Fig. 10. Biplots produced by discriminant analysis of morphometric data on first lower molars of four recent vole species and fossil material from sites Villány 6 and Villány 8 (a). Biplot produced by discriminant analysis of all studied fossil samples (b).

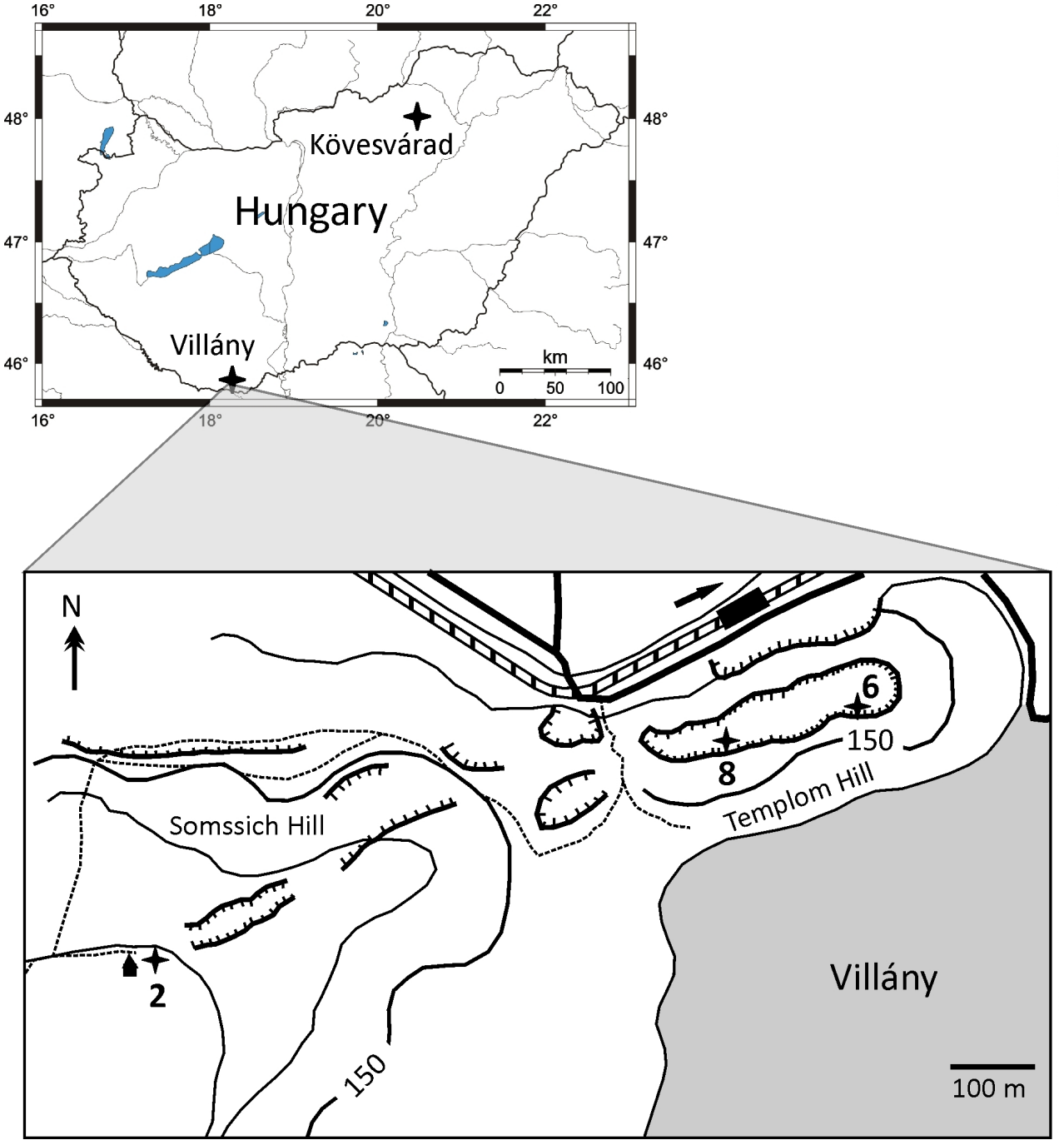
Fig. 11. Dendrogram produced by hierarchical clustering of morphometric data on first lower molars of all studied fossil voles specimens.

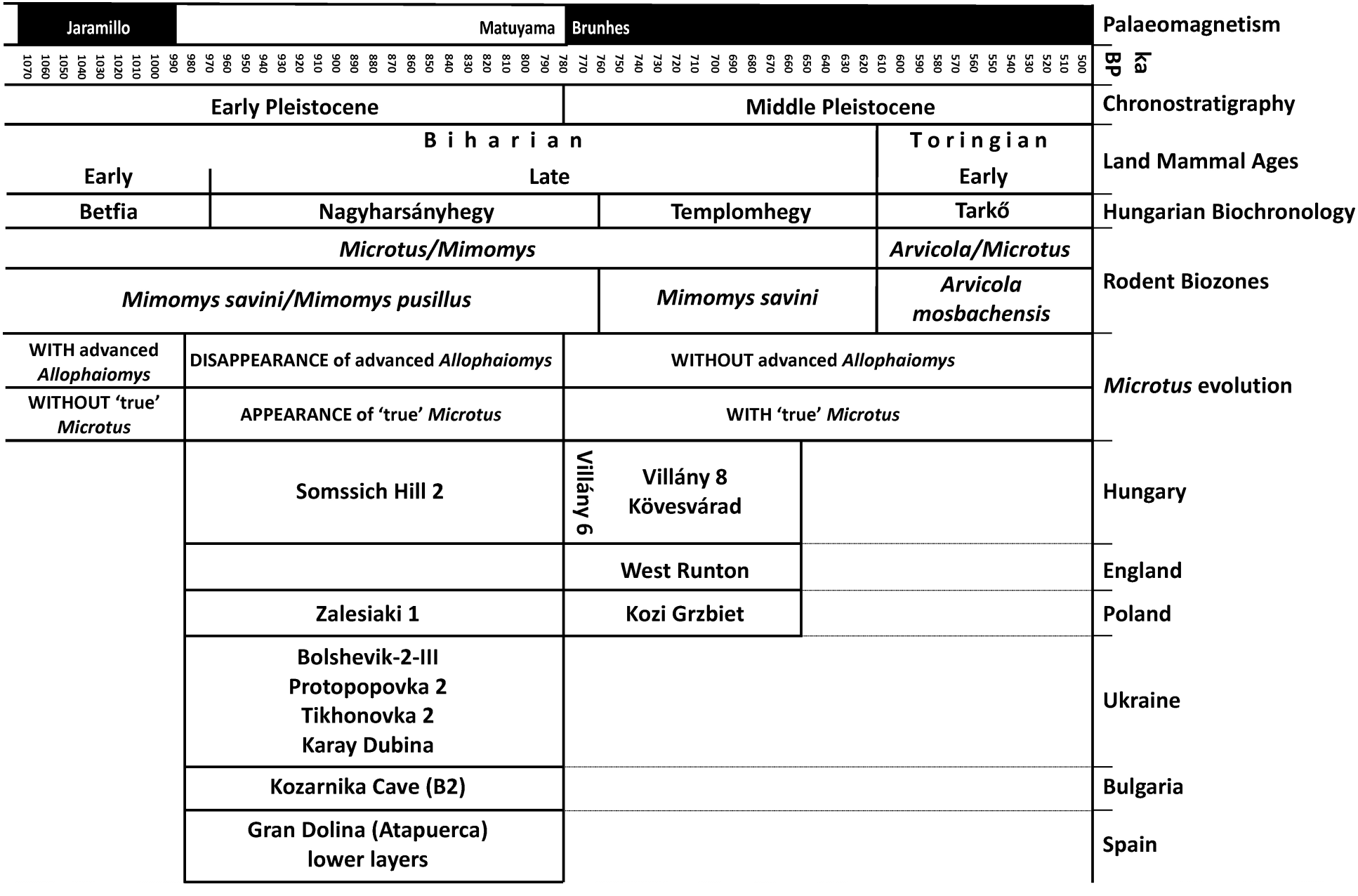
Fig. 12. Relative warp analysis of landmark data on first lower molars four recent vole species and fossil material from the Somssich Hill 2 site (a). The same analysis on the four recent specimens and fossil material from sites Villány 6, Villány 8 and Kövesvárad (b).

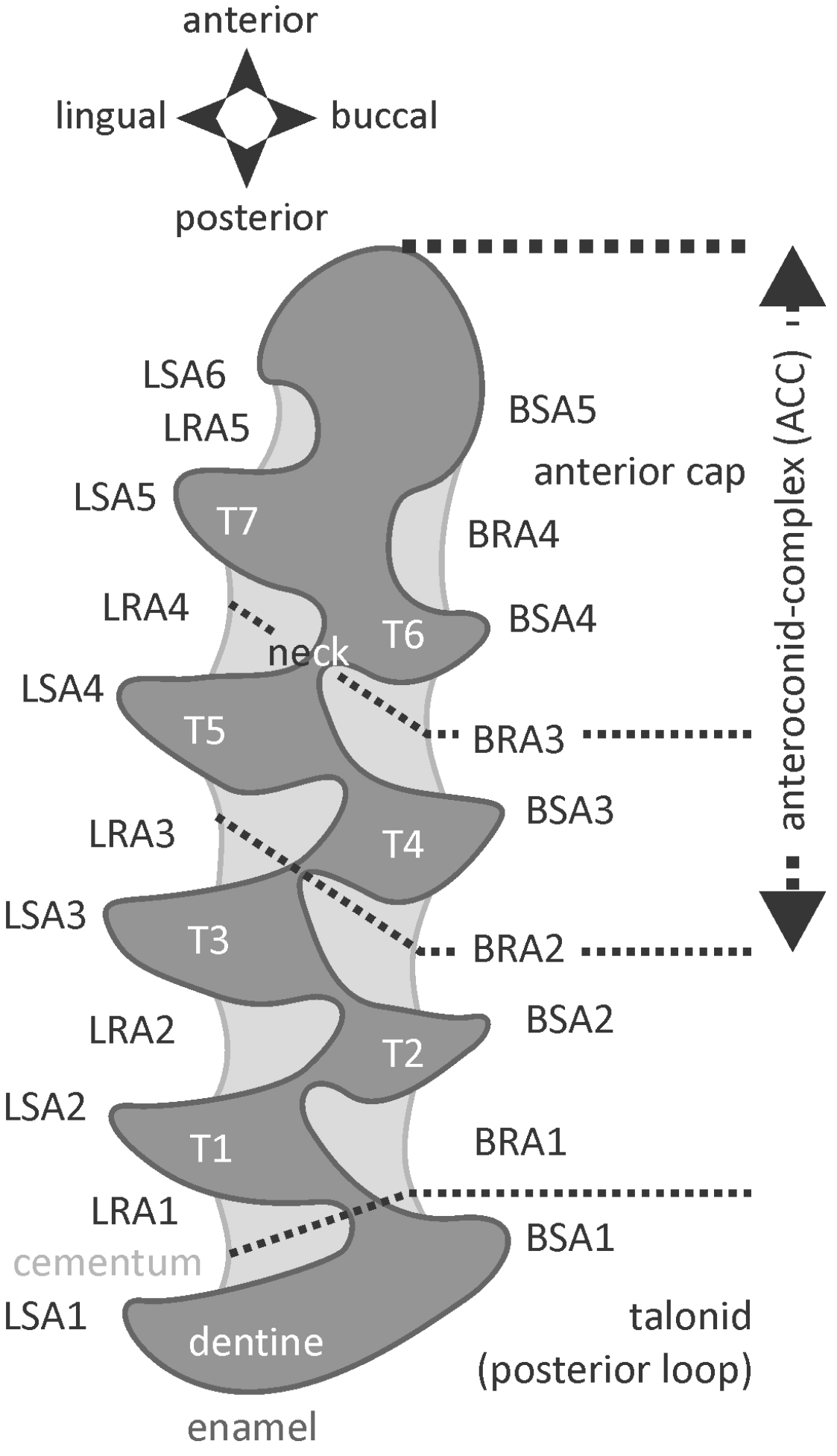
Fig. 13. Morphological variability of first lower molars of the five studied recent vole species and of *Microtus nivaloides* specimens from the Somssich Hill 2 site. Note the morphological plasticity of *M. nivaloides* that shows gradual transitions towards all recent species studied here.

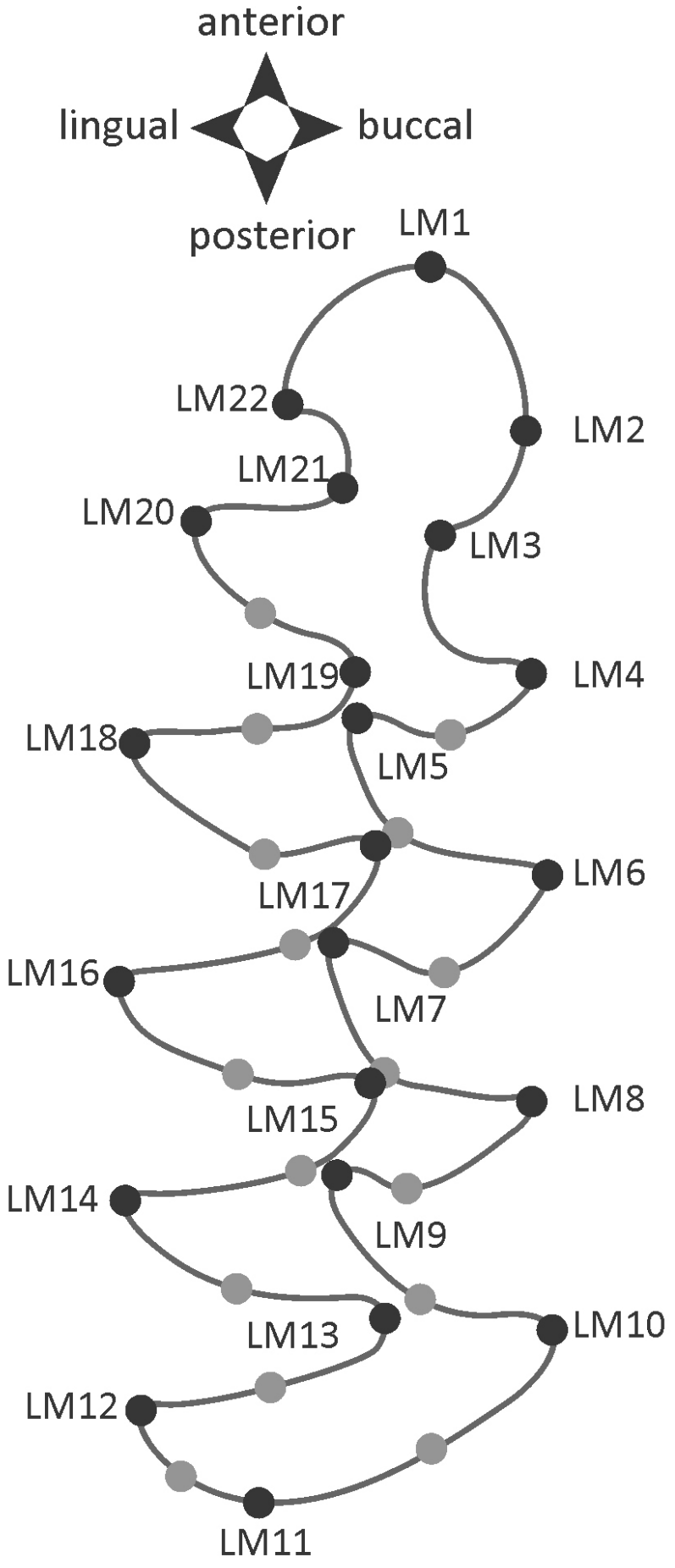
Fig. 14. Consensus shapes of *Microtus nivaloides* from the Somssich Hill 2 site, *M. nivalinus* from sites Villány 6 and Villány 8, as well as recent *M. arvalis*, *M. oeconomus* and *Chionomys nivalis*. The most characteristic features of the occlusal morphology are indicated by arrows.

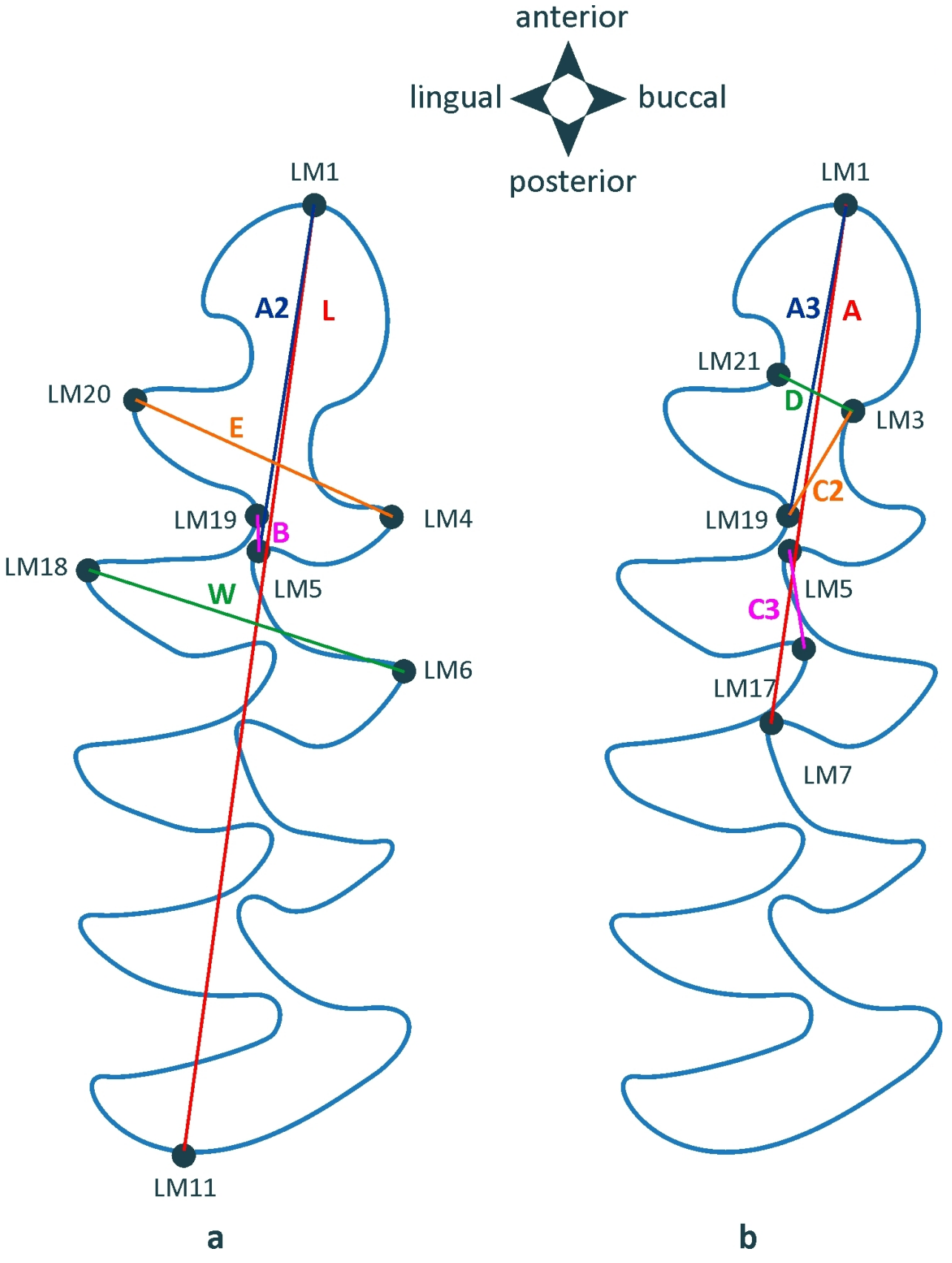
Fig. 15. Stratigraphically constrained phylogenetic relationships postulated for Early Pleistocene to recent vole taxa.

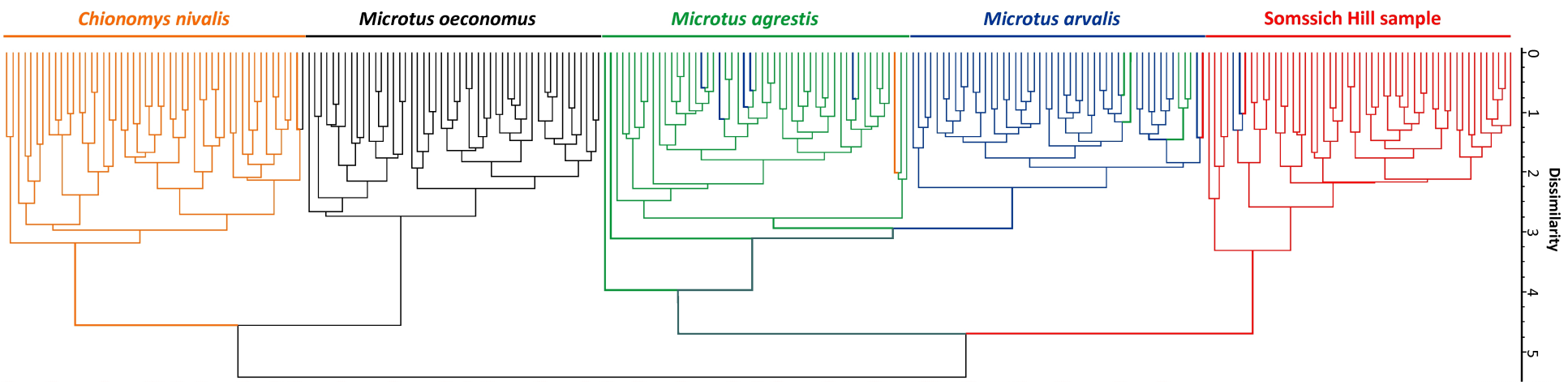

16°
18°
20°
22°
48°
47°
46°
Kövesvárad
Hungary
Villány
km
0
50
100
N
6
8
150
Templom Hill
Somssich Hill
2
150
Villány
100 m

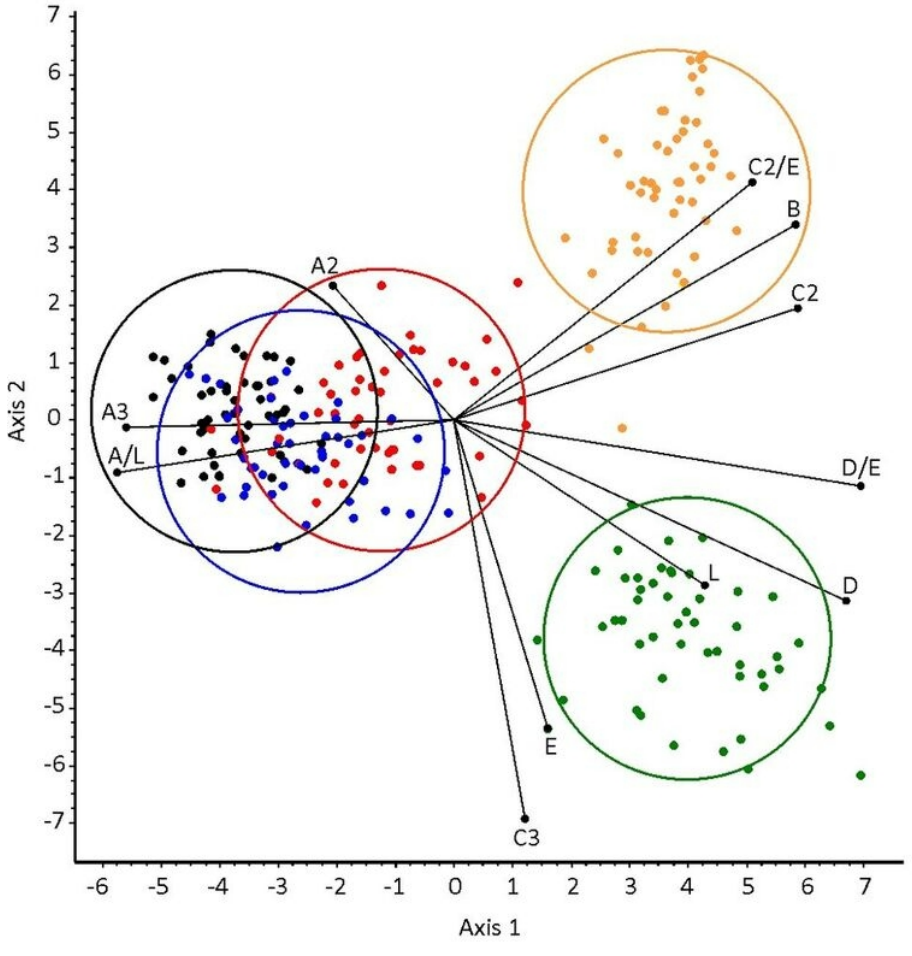

Jaramillo
Matuyama
Brunhes
Palaeomagnetism
1070 1060 1050 1040 1030 1020 1010 1000 990 980 970 960 950 940 930 920 910 900 890 880 870 860 850 840 830 820 810 800 790 780 770 760 750 740 730 720 710 700 690 680 670 660 650 640 630 620 610 600 590 580 570 560 550 540 530 520 510 500
ka BP
Early Pleistocene
Middle Pleistocene
Chronostratigraphy
Biharian
Toringian
Early
Late
Early
Land Mammal Ages
Betfia
Nagyharsányhegy
Templomhegy
Tarkő
Hungarian Biochronology
Microtus/Mimomys
Arvicola/Microtus
Mimomys savini/Mimomys pusillus
Mimomys savini
Arvicola mosbachensis
Rodent Biozones
WITH advanced Allophaiomys
DISAPPEARANCE of advanced Allophaiomys
WITHOUT advanced Allophaiomys
WITHOUT 'true' Microtus
APPEARANCE of 'true' Microtus
WITH 'true' Microtus
Microtus evolution
Somssich Hill 2
Villány 6
Villány 8
Kövesvárad
Hungary
West Runton
England
Zalesiaki 1
Kozi Grzbiet
Poland
Bolshevik-2-III
Protopopovka 2
Tikhonovka 2
Karay Dubina
Ukraine
Kozarnika Cave (B2)
Bulgaria
Gran Dolina (Atapuerca)
lower layers
Spain

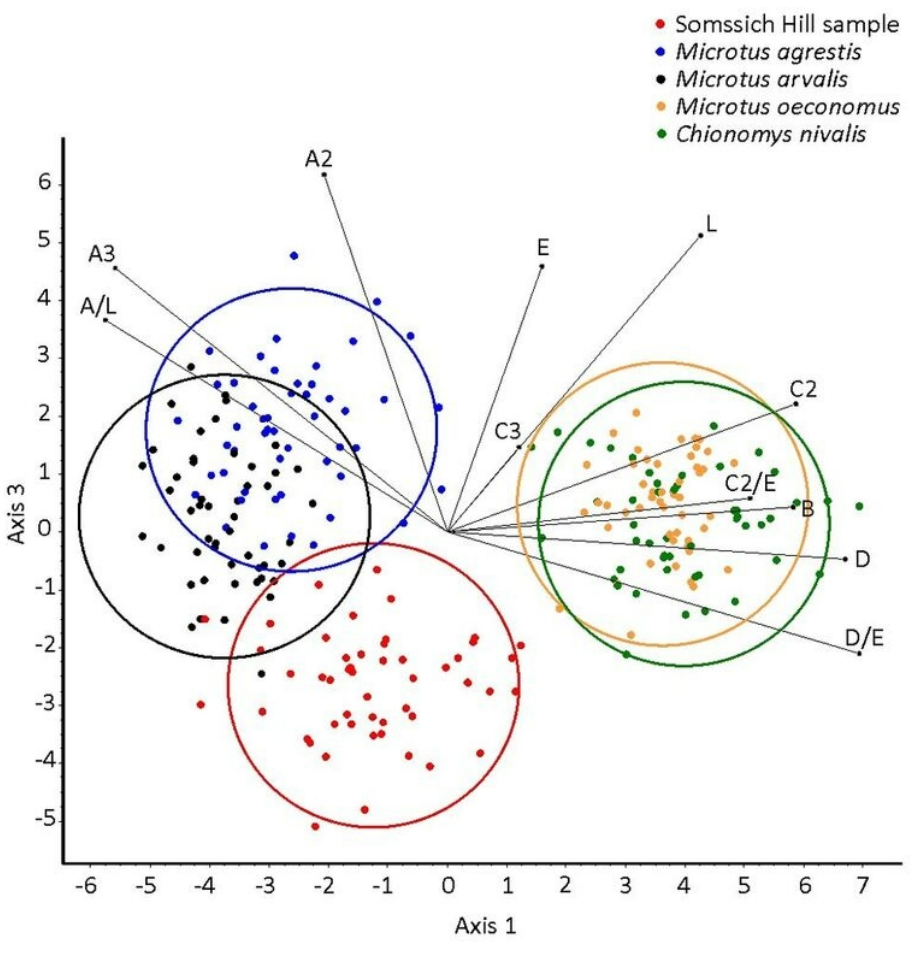

anterior
lingual
buccal
posterior
LSA6
LRA5
BSA5
anterior cap
LSA5
T7
BRA4
LRA4
T6
BSA4
neck
LSA4
T5
BRA3
BSA3
LRA3
T4
LSA3
T3
BRA2
LRA2
BSA2
T2
LSA2
T1
BRA1
LRA1
BSA1
cementum
LSA1
dentine
talonid
(posterior loop)
enamel
anteroconid-complex (ACC)

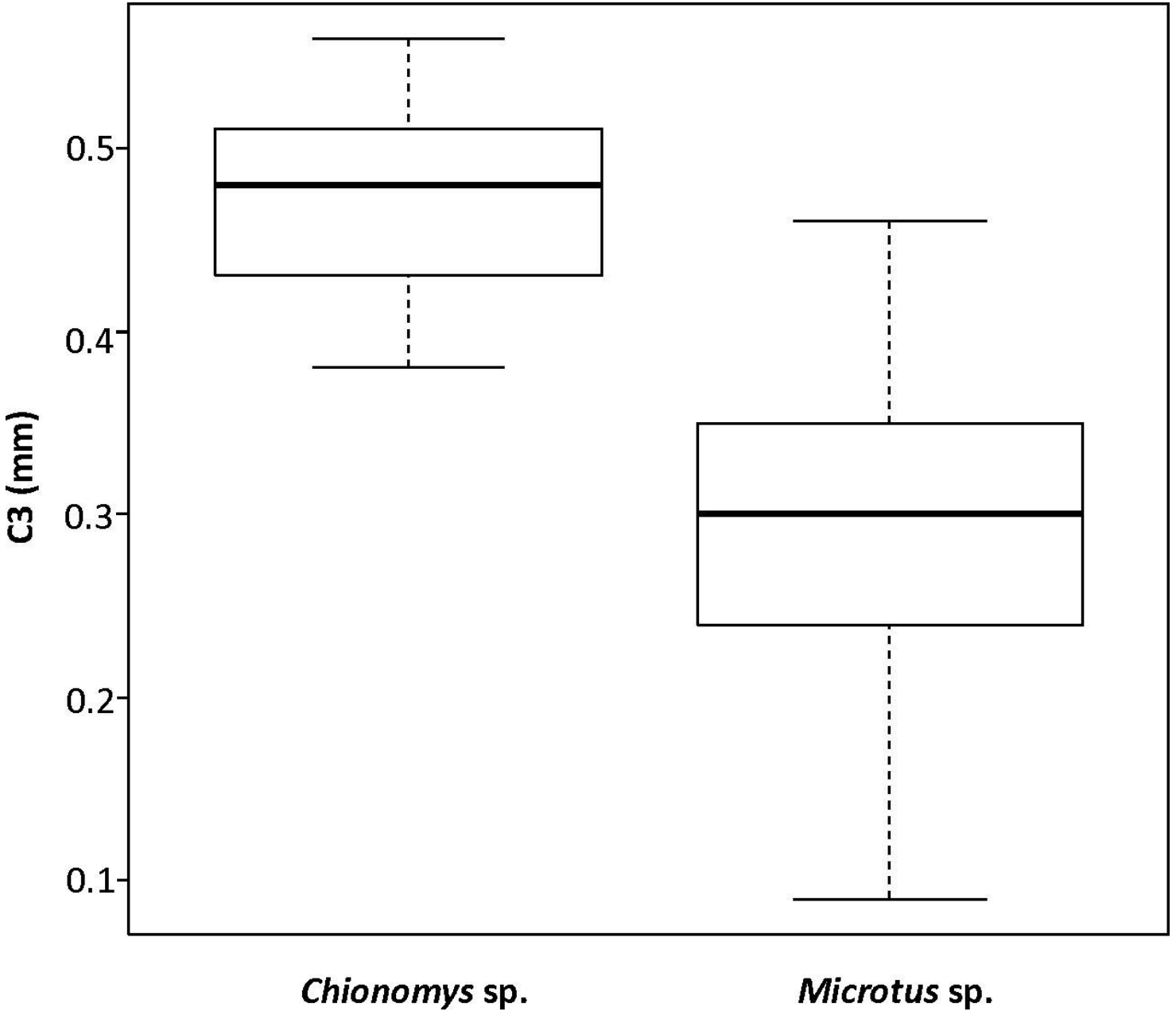

anterior
lingual
buccal
posterior
LM1
LM2
LM3
LM4
LM5
LM6
LM7
LM8
LM9
LM10
LM11
LM12
LM13
LM14
LM15
LM16
LM17
LM18
LM19
LM20
LM21
LM22

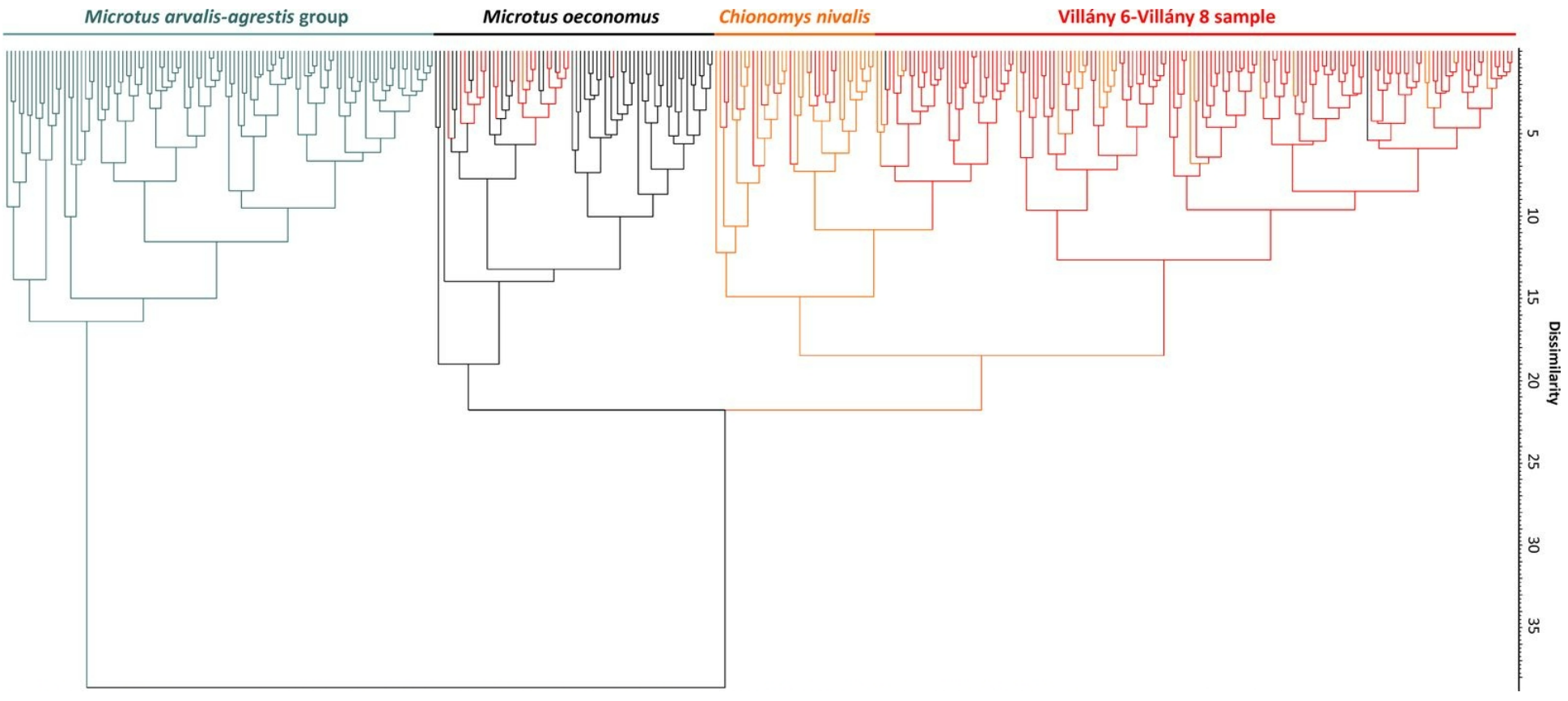

anterior
lingual
buccal
posterior
LM1
A2
L
LM20
E
LM19
B
LM4
LM18
W
LM5
LM6
LM11
a
LM1
A3
A
LM21
D
LM3
C2
LM19
LM5
C3
LM17
LM7
b

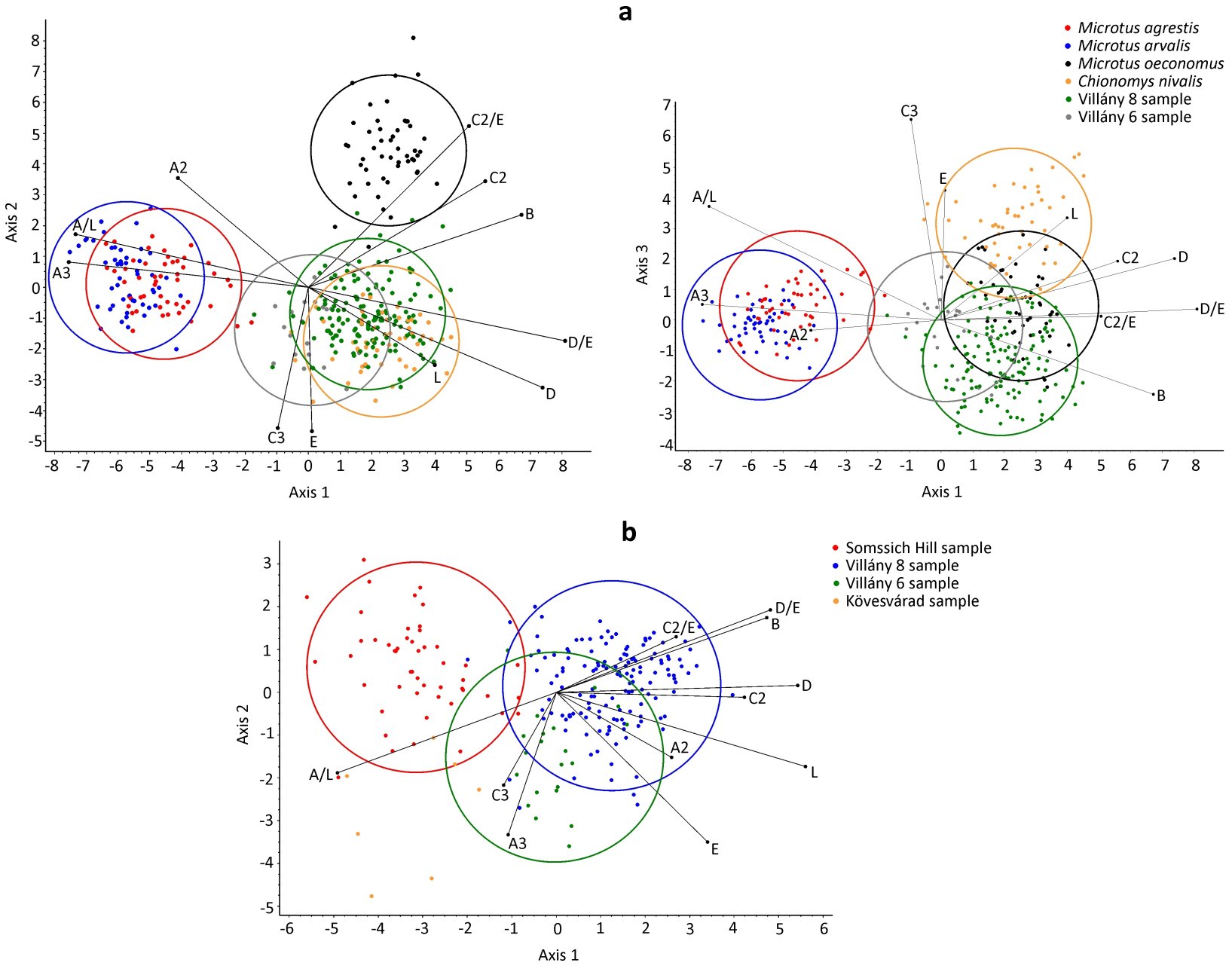

Chionomys nivalis
Microtus oeconomus
Microtus agrestis
Microtus arvalis
Somssich Hill sample
Dissimilarity
0
1
2
3
4
5

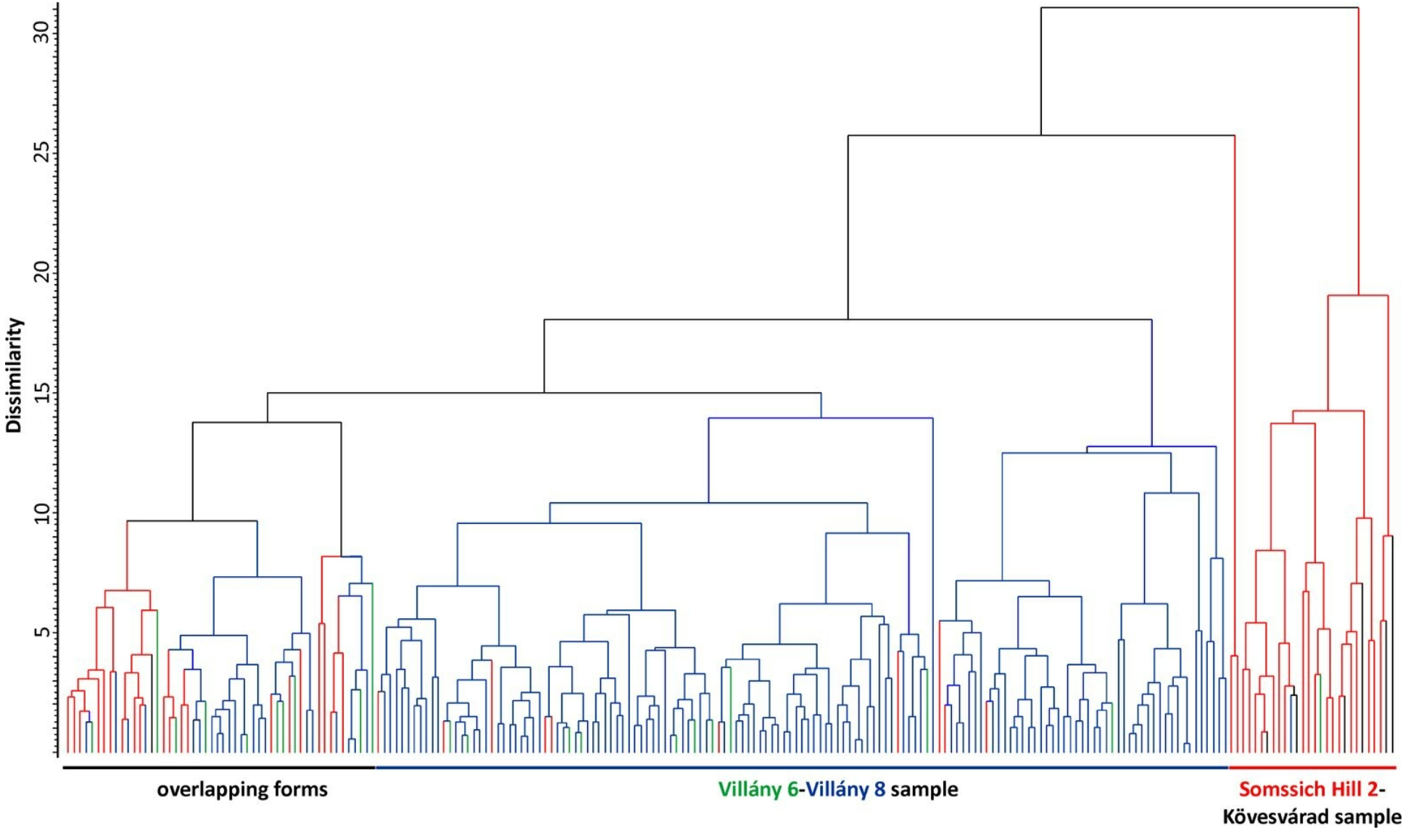

Axis 2
Axis 1
A2
A3
A/L
C2/E
B
C2
D/E
D
L
E
C3

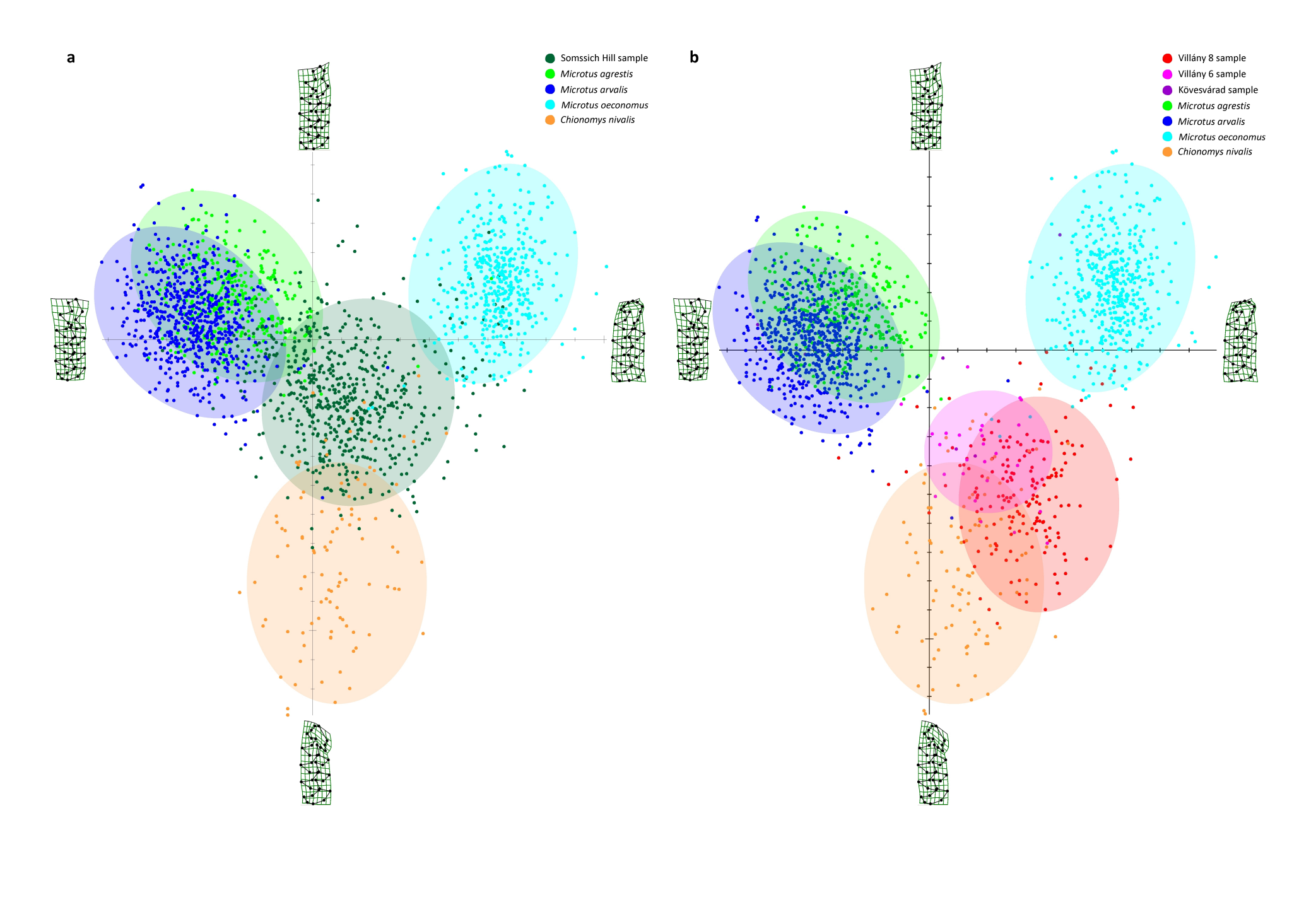

Somssich Hill sample
Microtus agrestis
Microtus arvalis
Microtus oeconomus
Chionomys nivalis
Axis 3
Axis 1
A2
A3
A/L
E
L
C2
C3
C2/E
B
D
D/E

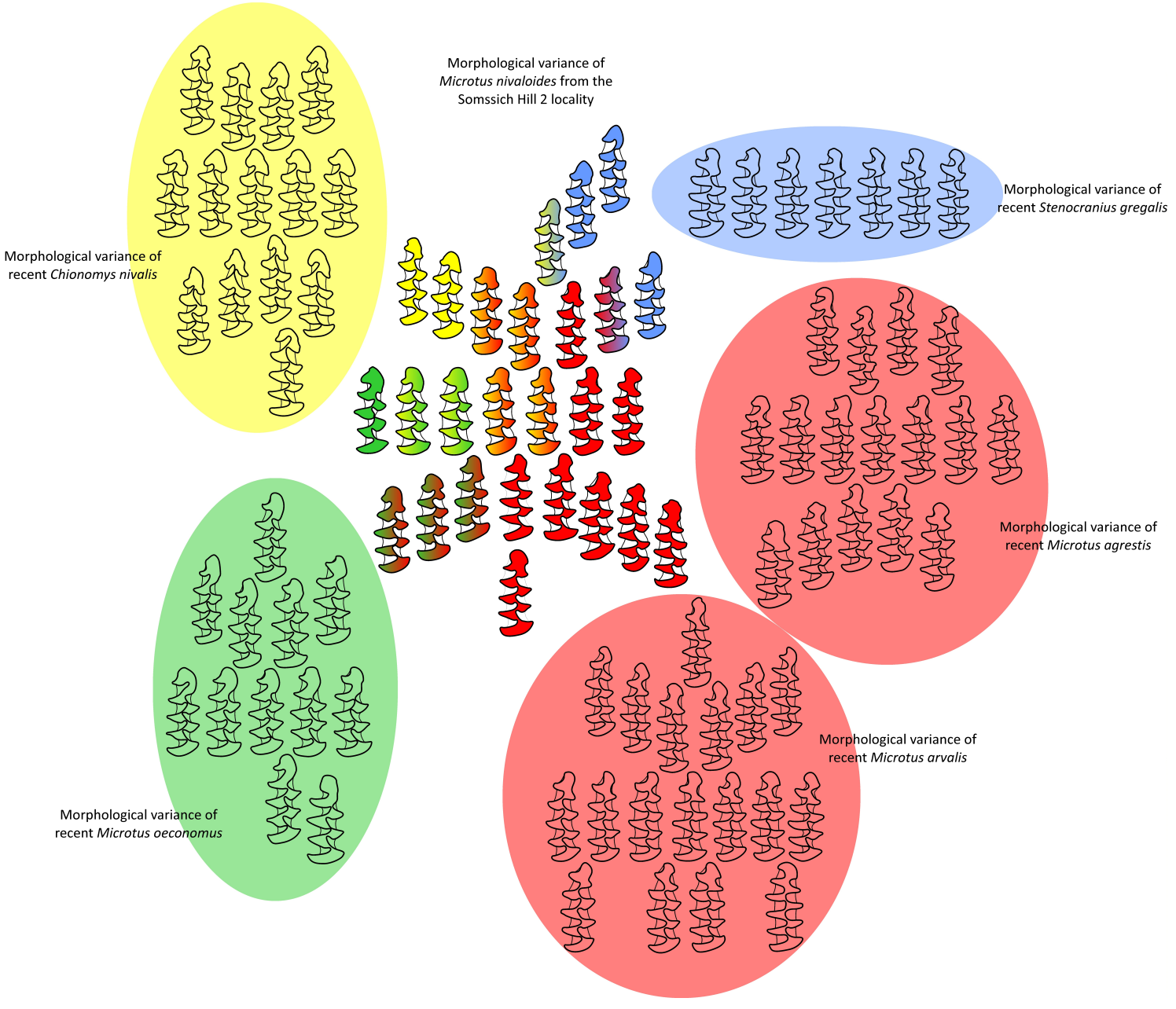

0.5
0.4
0.3
0.2
0.1
C3 (mm)
*Chionomys* sp.
*Microtus* sp.


Microtus arvalis-agrestis group
Microtus oeconomus
Chionomys nivalis
Villány 6-Villány 8 sample
5
10
15
20
25
30
35
Dissimilarity

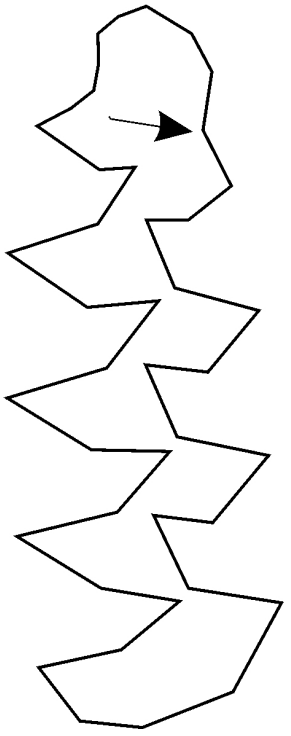

a
Axis 2
Axis 1
A/L
A2
C2/E
C2
B
A3
D/E
L
D
C3
E
Axis 3
Microtus agrestis
Microtus arvalis
Microtus oeconomus
Chionomys nivalis
Villány 8 sample
Villány 6 sample
b
Somssich Hill sample
Villány 8 sample
Villány 6 sample
Kövesvárad sample


Dissimilarity
30
25
20
15
10
5
overlapping forms
Villány 6-Villány 8 sample
Somssich Hill 2-
Kövesvárad sample

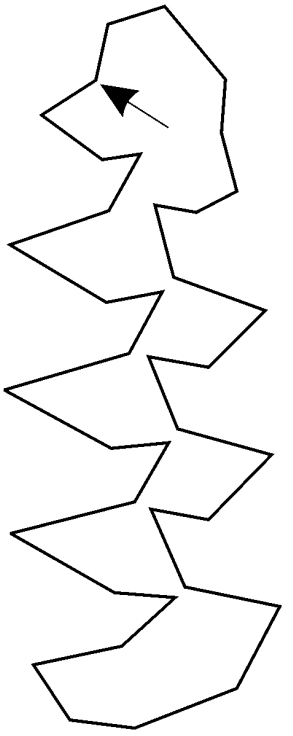

a
Somssich Hill sample
Microtus agrestis
Microtus arvalis
Microtus oeconomus
Chionomys nivalis
b
Villány 8 sample
Villány 6 sample
Kövesvárad sample
Microtus agrestis
Microtus arvalis
Microtus oeconomus
Chionomys nivalis


Morphological variance of *Microtus nivaloides* from the Somssich Hill 2 locality
Morphological variance of recent *Chionomys nivalis*
Morphological variance of recent *Stenocranius gregalis*
Morphological variance of recent *Microtus agrestis*
Morphological variance of recent *Microtus arvalis*
Morphological variance of recent *Microtus oeconomus*

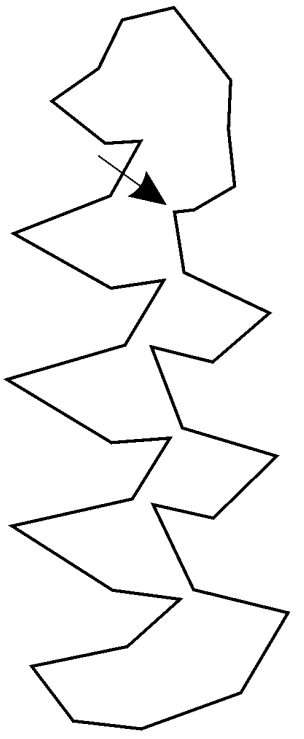
consensus shape of *M. nivaloides* from Somssich Hill 2

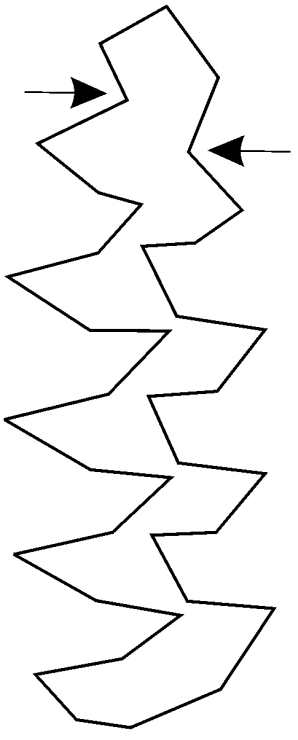


consensus shape of *M. nivalinus* from Villány 6

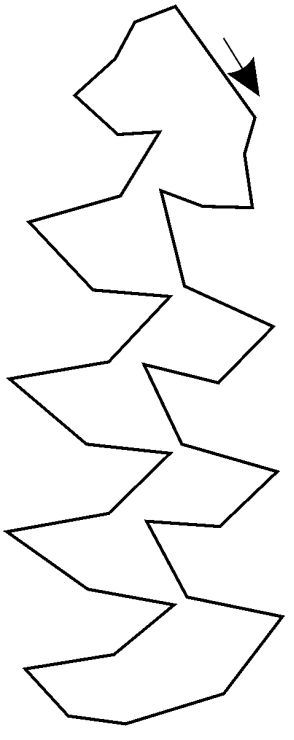


from Villány 8

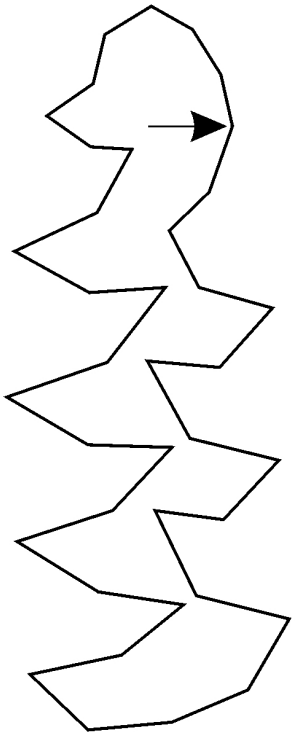




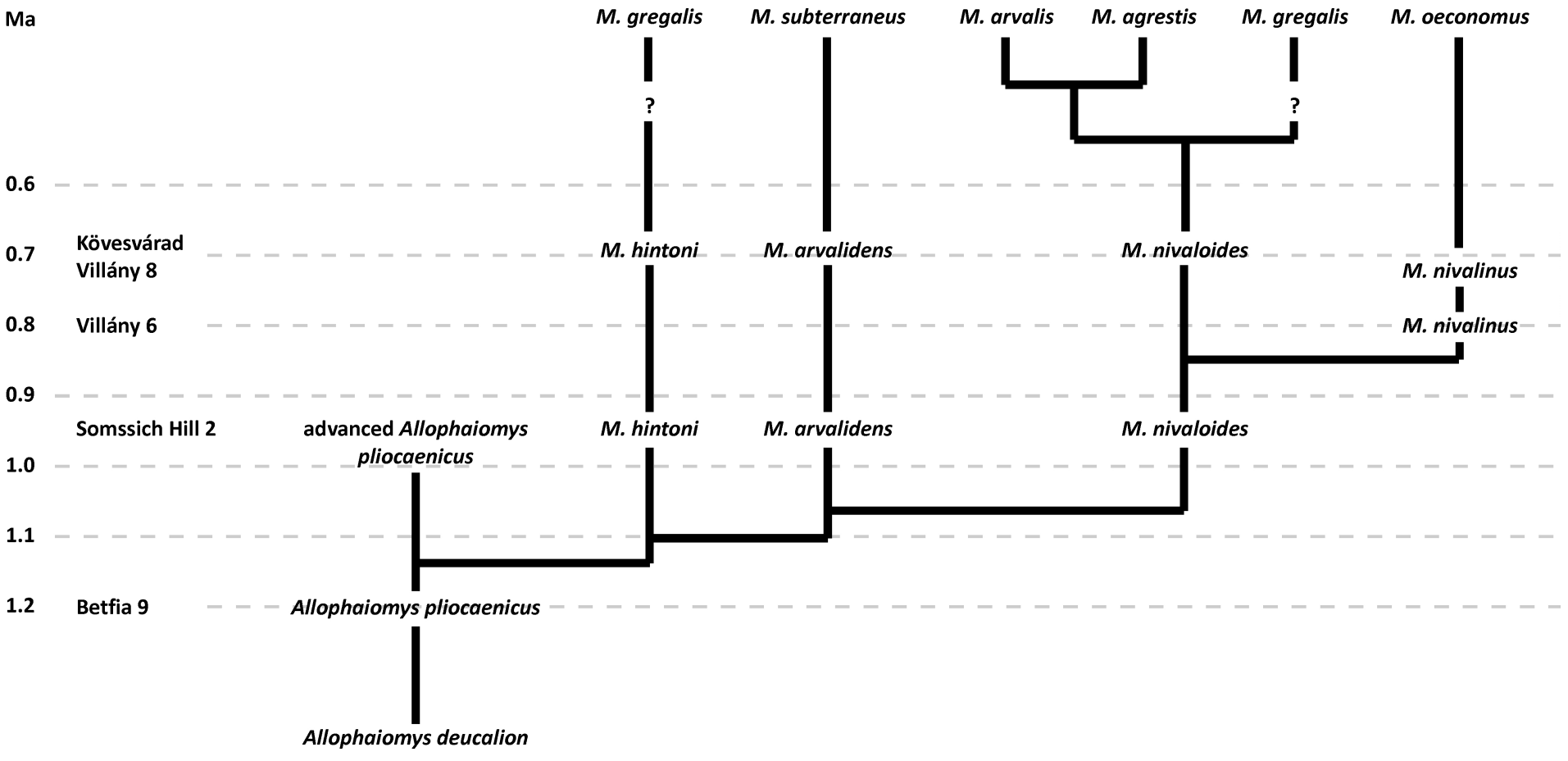
consensus shape of *Microtus arvalis*



consensus shape of *Chionomys nivalis*



consensus shape of *M. oeconomus*


Ma
M. gregalis
M. subterraneus
M. arvalis
M. agrestis
M. gregalis
M. oeconomus
?
?
0.6
0.7
Kövesvárad
Villány 8
M. hintoni
M. arvalidens
M. nivaloides
M. nivalinus
0.8
Villány 6
M. nivalinus
0.9
Somssich Hill 2
advanced Allophaiomys pliocaenicus
M. hintoni
M. arvalidens
M. nivaloides
1.0
1.1
1.2
Betfia 9
Allophaiomys pliocaenicus
Allophaiomys deucalion