Geometric morphometry of the upper molars in European wood mice *Apodemus*

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A b s t r a c t . We studied phenotypic relationships among six European *Apodemus* species (*A. agrarius, A. epimelas, A. flavicollis, A. sylvaticus, A. uralensis,* and *A. alpicola*) using landmark based morphometrics. Cartesian coordinates of 14 landmarks were recorded on the occlusal projection of upper molars from 175 specimens. Results revealed *A. agrarius* as the most distinct, having long and slender molars. Since primitive members of the genus (*A. atavus, A. orientalis, A. dominans*) are characterised by broad and robust molars, we conclude that *A. agrarius* is the most derived in this respect. Within the *Sylvaemus* subgenus/species group *A. epimelas* differed from the remaining four species in having more robust molars and a relatively longer second molar. Within the remaining four species two clusters emerged, although differences between them were slight. The *flavicollis-sylvaticus* tandem exhibited a relatively shorter second molar and more robust first molar. In five *Sylvaemus*, the robustness of molars correlated negatively with molar size, suggesting that between-species differences in molar shape result from allometric relations.

Introduction

The European wood mice *Apodemus* are, with few exceptions, a collection of sibling species and the relationships within the subgenus *Sylvaemus* remained poorly understood until very recently. The taxonomy progressed only after the application of biochemical and molecular techniques, occasionally complemented by careful morphological studies (see for reviews M u s s e r & C a r l e t o n 1993, H i l l e et al. 2002). In traditional taxonomy, size was the main morphological trait used to distinguish siblings (E l l e r m a n & M o r r i s o n - S c o t t 1966). Within this framework dental measurements were also utilised, mainly expressed either as the molar row length (M i l l e r 1912, and numerous subsequent authors), or the distance between the incisor and the third molar (D e m e t e r & L á z á r 1984). H a i t l i n g e r & R u p r e c h t (1967) attempted to evaluate the taxonomic value of linear tooth measurements in the subgenus *Sylvaemus*, but found this set of characters to be of limited use. On the other hand, several recent studies have revealed significant differences in measurements of individual molars among closely related species or even at the infraspecific level (V o h r a l í k 2002, V o h r a l í k et al. 2002). Furthermore, the morphology of molar cusps and ridges provides reliable taxonomic character among several species resembling each other very closely in other morphological traits (S t o r c h 1977,

Storch & Lütt 1989, Filippucci et al. 1996). In this paper we aim to evaluate differentiation among six European *Apodemus* species as revealed by geometric morphometrics of the upper molar landmarks, an approach which has not being attempted to date.

Traditional morphometrics (sensu Marcus 1993) of *Apodemus* molars is restricted to univariate comparisons of individual linear measurements or to bivariate plots of molar breadth against length (e.g. Tchernov 1979, Vohralík 2002). Geometric morphometrics has several advantages over the traditional approach, e.g. in partitioning size from shape for separate analysis and in providing a graphic way of locating and comparing the variability in different parts of the shape among studied groups (Corti et al. 2001). It uses all the information available about the landmark location, while rigorously adhering to the geometric definition of shape (Loy et al. 1996). Landmarks of homologous points allow the visualisation of shape changes from specimen to specimen (Capanna et al. 1996). We adopted a Thin Plate Spline (Bookstein 1991) approach, which is an interpolating method allowing statistical evaluation and the visualisation of shape differences through deformation of a grid.

We expected from our analysis to allocate specimens according to the similarity of the upper molars on the base of their shape. Assuming that molar shape includes phylogenetic information we predicted that species should form clusters based at least on their taxonomic allocation to subgenera or species groups (sensu Musser et al. 1996). This would make molar shape a useful tool in reconstructing phylogenetic relations within the group. As shown by Hille et al. (2002), phylogenetic trees based on biochemical and molecular data differ in their topologies. Since only a single tree topology can reflect the true evolutionary history of the group (Hille et al. 2002), there is clearly a need to analyse alternative sources of data. Molar morphology seems particularly suitable for such purposes, as it is the only structure allowing also inclusion of fossil taxa (cf. Dam 1996).

Material and Methods

We studied upper molars in 175 specimens of European wood mice (genus *Apodemus*) belonging to six species (sample sizes in parentheses): *A. agrarius* (Pallas, 1771) (Slovenia: vicinity of Nova Gorica, N=26), *A. epimelas* (Nehring, 1902) (littoral Dalmatia and Montenegro, N=36), *A. flavicollis* (Melchior, 1834) (Slovenia: Mt. Kočevski Rog, N=31), *A. sylvaticus* (Linnaeus, 1758) (Slovenia: Sečoveljske soline and Kranjska Gora, N=26), *A. uralensis* (Pallas, 1811) (Czech Repulic: Hodonin, N=24), and *A. alpicola* Heinrich, 1952 (Austria: Vorarlberg, N=32). Specimens originated from the collections of Naturhistorisches Museum Wien, Vienna (part of *A. alpicola*), Forschungsinstitut und Natur Museum Senckenberg, Frankfurt a/M (part of *A. alpicola*), Institute of Vertebrate Biology, ASCR Brno (*A. uralensis*), and Slovenian Museum of Natural History, Ljubljana (the rest). *Apodemus agrarius* is the only representative of the subgenus/species group *Apodemus*, while all the remaining taxa are from the subgenus/species group *Sylvaemus* (cf. Musser et al. 1996). Within the former, *A. epimelas*, which is the most distinct, is occasionally considered to be a member of the subgenus *Karstomys* (cf. Niethammer & Krapp 1978); regardless of its formal assignation, molecular evidence suggests association of *A.epimelas* with *Sylvaemus* to be weak (Michaux et al. 2002).

Discrimination of *Sylvaemus* siblings can be difficult in some cases. All our material was determined on the basis of morphological characters, using diagnostics by Tvrtković (1979) and Storch & Lütt (1989). Any doubtfull cases have been excluded.

To make results of multivariate statistics comparable, samples were selected to be of approximately equal size (i.e. between 24 and 36). Each species was represented by

a sample obtained from a single location or from a restricted region. This eliminated the effect of geographic variation which is considerable in some of the taxa studied (e.g. A l c á n t a r a 1991).

Although dental tissues are not modified much after being deposited (H i l s o n 1990), juveniles and senile specimens (with a higher degree of toothwear) were excluded. We also considered only skulls with molars firmly in alveoli to avoid error in sampling landmarks which were on the contact of two adjacent molars (landmarks nos. 4, 6, 9, and 11).

For each specimen 14 landmarks were collected on the occlusal projection of the left upper molars' row (Fig. 1). Each skull was placed under a TV camera connected to a personal computer. Images were digitised and landmarks were collected using the software tps Dig (R o h l f 2001). In order to avoid bias due to measurement errors, 30 *A. alpicola* specimens were measured twice independently at >24-h intervals. All the landmarks showed good repeatability. Because of significant size differences among species, the 175 scaled configurations were then superimposed so as to unite centroid size and then centred and rotated in order to minimise the scatter of landmarks (A u f f r a y et al. 1996). This was done using the Procrustes generalised least square superimposition (GLS; B o o k s t e i n 1991, R o h l f 1993). Further analysis was based on consensus configuration (all individual mean configuration). Each of the 175 landmarks configurations was superimposed, case by case, on the mean form. Thin Plate Spline Relative Warp program (TPSRW, R o h l f 2002) was used to extract the relative warp scores (for details see R o h l f 1993, 1999). Relative warps adhere to the geometric definition of shape and are free of size effect. This suited our aims since we did not search for differences among species in size, a topic frequently dealt with in taxonomic papers (see above). Relative warp scores were tested for homogeneity of variance. Since no such deviation was detected in any of the relative warps (not significant), they were all introduced into further uni- and multivariate statistics to detect variations among groups. Overall similarity in molar shape among species was assessed by Discriminant Function Analysis (DFA). Rectangular matrix of squared Mahalanobis distances (D^2) was used to construct a similarity tree based on UPGMA (Unweighted pair-group method, arithmetic
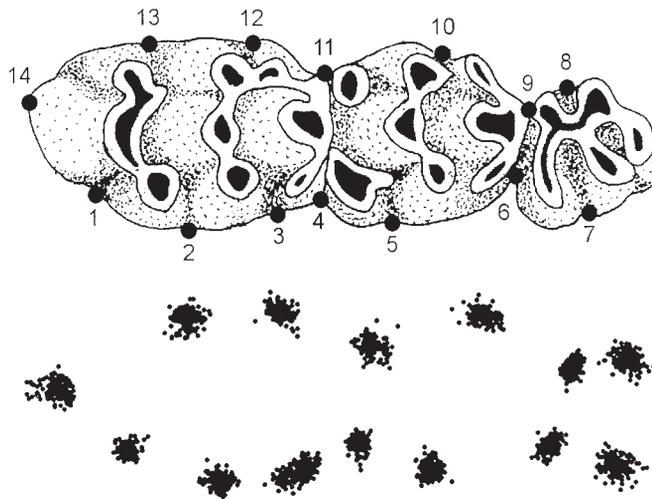
Fig. 1. Landmarks recorded on the occlusal surface of the *Apodemus* upper molars (above). Projection of landmark locations for all specimens, after General least square alignment (below). Anterior is to the left and lingual is below.

average) and Minimum Spanning Tree (S n e a t h & S o k a l 1973). Centroid sizes were extracted using tpsRegr programme (R o h l f 2000). Centroid size is the square root of the sum of squared distances from the landmarks to the centroid of the landmarks. In the absence of allometry, it is the only size measure that is uncorrelated with all shape variables and as such a measure of an overall size (R o h l f 2002). Statistical tests were run using STATISTICA analysis system (Release 5.5 '99) and NT-SYS (R o h l f 1998) programmes.

Results

Centroid size (a measure of overall molar size) differed significantly among species (One Way ANOVA $F_{5,169}$ = 448.1 p < 0.01; Fig. 2). *Apodemus epimelas* was the biggest, being followed by *A. flavicollis*, while *A. uralensis* appeared the smallest in this respect. These results are not surprising since molar size evidently corresponds to general body size. There was no significant difference between sexes in size (F values for centroid size ranged between 0.22 and 0.83, not being significant; p >> 0.05).

The first three relative warps (RW) derived from case by case superimposition of the 175 landmark configurations on the mean form explained nearly half of the original variance (=47.9 %). As the first step we checked relative warps for sex dimorphism. In each of the three species analysed (*A. epimelas, A. uralensis* and *A. alpicola),* ANOVA detected only two relative warps per species to be significantly different (F > 4.5, p < 0.05). However, secondary dimorphism evidently affected different parts of dentition in each species: relative warps RW3 and RW24 in *A. epimelas*, RW7 and RW8 in *A. uralensis*, and RW10 and RW18 in *A. aplicola*. In the absence of congruence across species, we ignored these differences and pooled sexes in subsequent analyses.

Discriminant function analysis (DFA) on relative warps classified 92.6 % of specimens into the correct group (Table 1). Classification results were the best for *A. agrarius* (100 % of specimens classified properly) while only 88 % of *A. sylvaticus* were classified as such. Values of the F matrix based on squared Mahalanobis distances and on F approximations of multivariate statistics ($F_{120, 722}$ = 13.9, p < 0.001 for Wilk's lambda = 0.0028; Table 2) confirmed the high discrimination among populations. All pairwise Mahalanobis distances differed significantly from zero (at p<0.01).
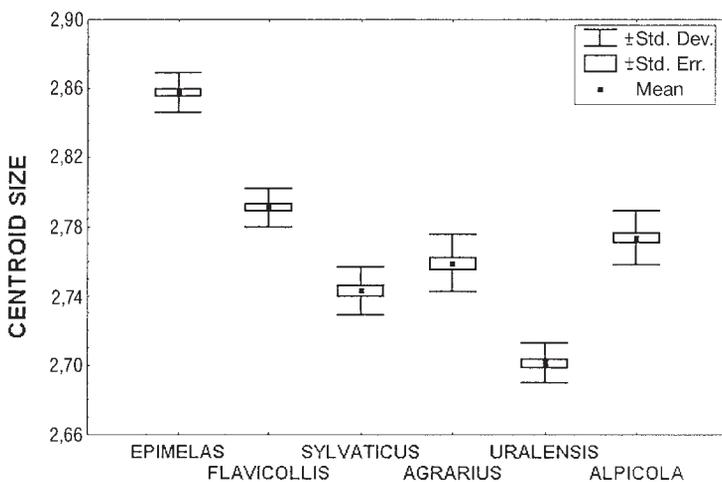

Fig. 2. Box plots of centroid size for six *Apodemus* species.

Table 1. Classification matrix derived from the Discriminant Function Analysis of six *Apodemus* species based on relative warp scores. Rows are actual groups and columns are predicted groups.

|	Percent Correct	1	2	3	4	5	6
1. *A. epimelas*	97.1	34	1	0	0	0	0
2. *A. flavicollis*	87.1	1	27	3	0	0	0
3. *A. sylvaticus*	88.0	0	2	22	0	1	0
4. *A. agrarius*	100.0	0	0	0	26	0	0
5. *A. uralensis*	91.7	0	0	1	0	22	1
6. *A. alpicola*	91.2	1	1	0	0	1	31
Total	92.6	36	31	26	26	24	32

Table 2. Mahalanobis Distances between six *Apodemus species*. Below the diagonal are corresponding F-values (df = 24, 147) with levels of significance: * p<0.01, ** p<<0.001.

	1	2	3	4	5	6
1. *A. epimelas*	0.000	21.14	31.52	54.75	41.01	26.22
2. *A. flavicollis*	12.21 **	0.000	9.41	55.31	25.89	16.17
3. *A. sylvaticus*	16.02 **	4.51 **	0.000	57.57	21.42	18.03
4. *A. agrarius*	28.58 *	27.33 *	25.52 *	0.000	64.34	67.75
5. *A. uralensis*	19.80 **	11.42 **	8.68 **	27.59 **	0.000	15.14
6. *A. alpicola*	15.63 **	8.93 **	8.98 **	34.69 **	7.37 **	0.000

Projection of specimens onto the first two discriminant function axes (explaining 74.0 % of cumulative variance in the original data set) is shown in Fig. 3. The first discriminant function (DF1; 48.0 % of variance explained) clearly separated between *A. agarius* on the one hand and the *Sylvaemus* species on the other, with *A. alpicola*'s centroid being at the greatest statistical distance from that of *A. agrarius*. Analysis of splines associated with extremes of variation revealed *A. agarius* as having long and slender molars while *Sylvaemus* species were characterised by broad molars. The first upper molar was particularly slender in *A. agrarius*, with a pronouncedly elongate anterior-most part (i.e. the cusp t2), and was also relatively longer than in *Sylvaemus*. The second molar of *A. agrarius* was clearly narrowed in its postero-labial part.

Distinction between *A. epimelas* and the remaining *Sylvaemus* mice was achieved along DF2 (explaining 25.9 % of variance). As revealed from splines analysis, differences between the extremes (*A. epimelas* v. *A. uralensis*) were not very pronounced. In general, *A. epimelas* tended towards more robust molars, and also a relatively longer second upper molar. In this respect, *A. agrarius* appeared distinct from *A. epimelas*, resembling more closely the remaining *Sylvaemus* species.

Phenetic relations among species are summarised as a UPGMA tree, derived from group centroids of squared Mahalanobis distances (Table 2, Fig. 4). The tree summarises 94 % of the information in the original matrix (cophenetic correlation coefficient r = 0.97, Mantel t = 2.3 $p_{ran. Z < obs. Z}$ = 0.99). As one could expect already from the dispersion of specimens along the first two discriminant axes, *A. agrarius* appeared to be the sister species to *Sylvaemus*. Within the subgenus *Sylvaemus*, *A. epimelas* hold the most basal position, *A. uralensis* clustered with *A. alpicola* and *A. flavicollis* clustered with *A. sylvaticus*. The *sylvaticus-flavicollis* and *uralensis-alpicola* clusters differed primarily along the DF3 with
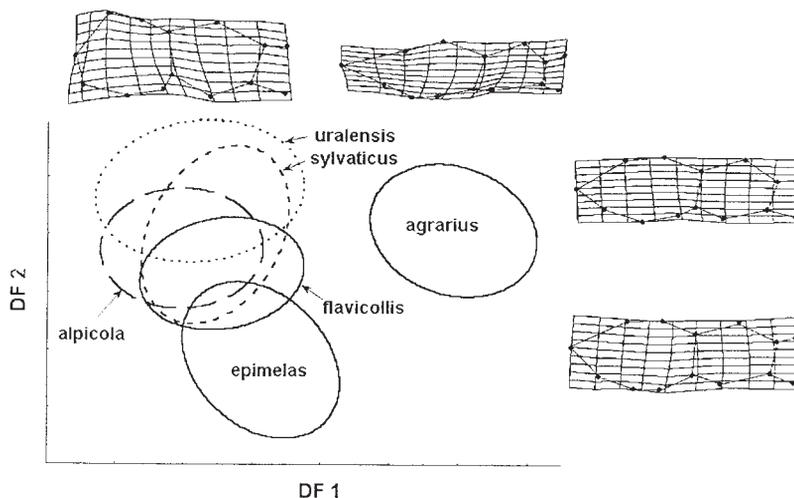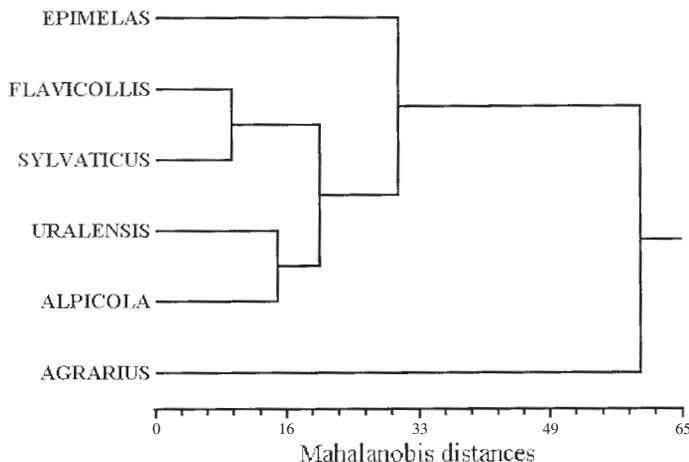
Fig. 3. Projection of specimens (95% confidence ellipses) onto the first and second discriminant functions (DFs) as derived from Discriminant Function Analysis of relative warps describing shape of the upper molar teeth. Shape changes associated with extremes of variation are shown as thin plate spline deformation grids.

the latter achieving higher scores (Fig. 5). Regardless of this, comparison of thin plate spline deformation grids (not shown) did not reveal much differentiation in molar shape along the DF3 axis. The most marked differences were the relatively shorter second upper molar and slightly more robust first molar in the *flavicollis-sylvaticus* tandem.

Allometric relationships

The five *Sylvaemus* species showed negative correlation between DF1 and DF2 scores ($r = -0.47$, $p < 0.0001$). Furthermore, these species were evidently allocated along DF2 according to their decreasing overall size, a factor not considered in the above analysis. *Apodemus epimelas*

Fig. 4. UPGMA tree based on the matrix of squared Mahalanobis distances among six *Apodemus* species as derived from Discriminant Function Analysis of relative warps describing shape of the upper molar teeth.

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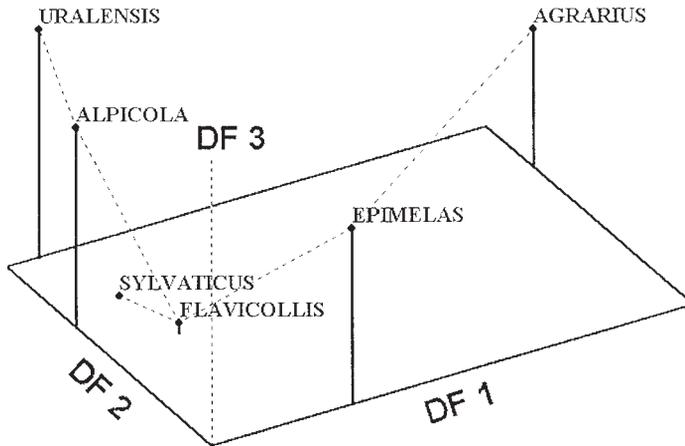
Fig. 5. Projection of group centroids for six *Apodemus* species onto the first three discriminant functions (88.6% of variance explained) as derived from Discriminant Function Analysis of relative warps describing shape of the upper molar teeth. Centroids are connected by the Minimum Spanning Tree.

(the largest) showed the lowest DF2 scores and *A. uralensis* (the smallest) achieved the highest scores. Plot of DF2 scores against centroid sizes (= measure of molar size) resulted in strong negative and highly significant correlation (r = -0.87, p << 0.001). This suggests that interspecific shape changes in *Sylvaemus* were due to allometry, thus the larger the molar tooth-row, the more robust the molars tended to be. Such a pattern was not repeated at the intraspecific level, where none of the correlation coefficients differed significantly from zero.

Discussion

Phenetic relations among the six *Apodemus* species as derived from molar morphology correspond to their traditional division into two main species groups (possibly subgenera): *Apodemus* and *Sylvaemus* (M u s s e r et al. 1996). Within *Sylvaemus*, *A. epimelas* proved to be the most distinct, which is again in agreement with results obtained from other data sets: external (M i l l e r 1912), cranial and dental (N i e t h a m m e r & K r a p p 1978), reproductive (glans penis and baculum; W i l l i a m s et al. 1980), biochemical (F i l i p p u c c i et al. 2002), and molecular (B e l l i n v i a et al. 1999, M i c h a u x et al. 2002). Relations among the remaining four 'brown' *Sylvaemus* species are more puzzling since different genetic character systems result in topologies which were not mutually congruent. As the available information does not allow firm conclusions to be made as to whether *A. sylvaticus* is a sister species of *A. flavicollis* or of *A. uralensis* (H i l l e et al. 2002), it would be groundless speculation to judge whether observed molar variation reflects phylogeny or might be due to convergent evolution among closely related taxa.

Considering the fact that the first upper molar of primitive fossil *Apodemus* species (e.g. *A. orientalis, A. dominans* and *A. atavus*) was broad and robust (F e j f a r & S t o r c h 1990, Ş e n 1977, S t o r c h 1987), the slender molar with an elongated anterioromedial cusp (t2) of *A. agrarius* is evidently an evolved character. Such a conclusion agrees with that of M u s s e r et al. (1996) that the *Apodemus* group (which also includes *A. agrarius*) is definable within the genus by at least one derived trait (i.e. supraorbital ridges) in addition to cusp reduction or loss. It seems that reduction of cusps was also associated with narrowing of molars.

Relations between *A. epimelas* and the remaining *Sylvaemus* species, which concern robustness of molars, are more puzzling. As molar robustness followed allometric relations with molar size, the more slender molars in the *alpicola-uralensis* cluster possibly reflect simply allometry, but might be also due to a phylogenetic impact. If the latter presumption holds, *A. epimelas* would be more primitive, a conclusion further supported by its less reduced second molar. More material should be studied before a firm conclusion on the allometric relations between molar size and their robustness could be established in *Sylvaemus*. Considering extensive size variation in some species, e.g. in *A. sylvaticus* (A l c á n t a r a 1991) and *A. flavicollis* (K r y š t u f e k & S t o j a n o v s k i 1996) the group certainly offers good possibilities in this respect.

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