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THREE DIMENSIONAL GEOMETRIC MORPHOMETRIC STUDY OF THE ETHIOPIAN *MYOMYS – STENOCEPHALEMYS* COMPLEX (MURINAE, RODENTTA).

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ABSTRACT - Geometric morphometrics was used to investigate the Ethiopian *Myomys – Stenocephalemys* complex, and to suggest possible explanations for differences in size and shape. The four species of the complex (*M. albipes, M. ruppi. S. griseicauda, S. albocaudata*) and a Kenyan species, *M. fumatus*, were studied using Procrustes analysis of three dimensional landmarks collected over the skull. All these species occur in very different habitats, from forests at 1000 m up to the Afro Alpine moorlands above 4000 m. There is a substantial contradiction between phylogenetic relationships based on chromosomal rearrangements and allozymes (two distinct lineages corresponding to the two genera), and mtDNA (*Stenocephalemys* being paraphyletic). Geometric morphometrics supports the former hypothesis. Partial Least-Squares analysis shows a significant relation between variation in size and shape and altitude, which strongly suggests that adaptation is a major causal factor for divergence in the morphology of the skull. Size increases with altitude, paralleling a clinal change in shape, which involves stenocephaly as characterising the highland species. This shape modification allows the rodents to scan the sky efficiently for birds, which represent the main category of predators in the Afro Alpine moorlands.

Key words: Geometric morphometrics, Procrustes analysis, *Myomys, Stenocephalemys,* African Rodents.

INTRODUCTION

Ethiopia is the African country with the highest average altitude and it is distinctive its high rate of endemism, Twenty one percent of the 70 rodent species known so far, are endemic (Yalden and Largen, 1992; Hillman, 1993; World Conservation Monitoring Centre, 1992) including two of the 7 *Myomys* species, *M. ruppi* and *M. albipes*, and the endemic genus *Stenocephulemys*, with the two species *S. griseicauda* and *S. albocaudata.*

These two genera have always been considered closely related to each other (Yalden et al., 1976), but they occur in very different environments. *M. albipes* is widespread over all of Ethiopia in forest blocks at altitudes ranging from 800 m up to 3300 m (Yalden et al., 1976; Afework Bekele and Corti, 1997) (Fig. 1). *M. ruppi,* another forest species described by Van der Straeten and Dieterlen (1983), has a distribution limited to the area of Bonke in the Gamo Gofa region (2700-3200 m). *S. griseicauda* and *S. albocaudata* are confined to the highlands above 3000 m asl. *S. albocaudata* is re-

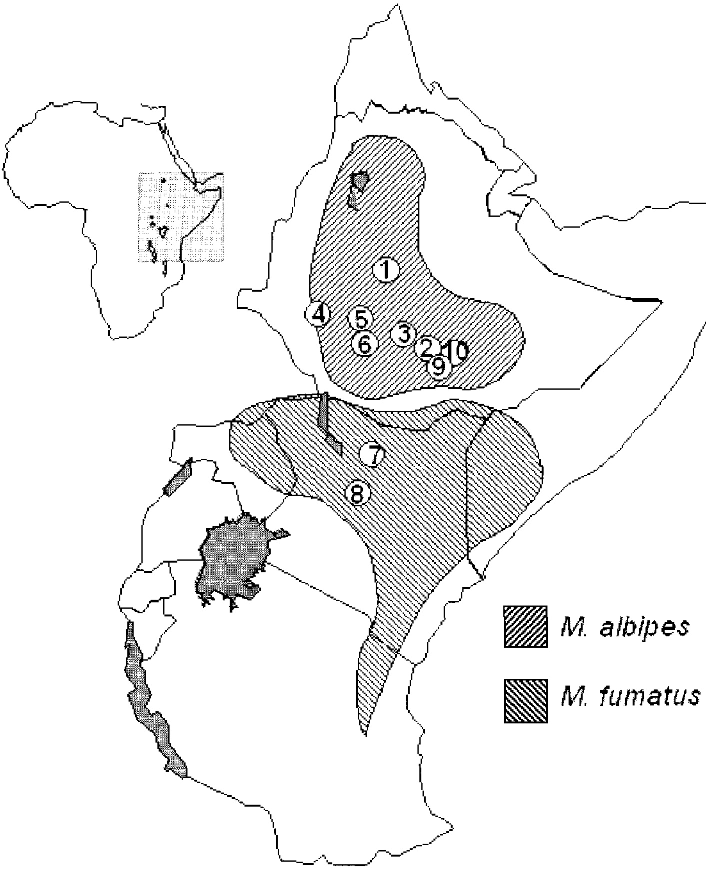

Figure 1- Map of East Africa and the Horn of Africa (enlargement of the area boxed), with the approximate ranges of *M. albipes* and *M. fumatus* and the location of the samples studied. *M. ruppi*, *S. griseicauda* and *S. albocaudata* ranges are not shown as they are very restricted. 1 = Addis Ababa; 2 = Dinshu; 3 = Sidamo; 4 = Godare: 5 = Bonke; 6 = Dorse; 7 = Marsabit; 8 = Mt. Suswa; 9 = Bale: 10 = Goba.

stricted to the afro-alpine moorland of the Bale plateau. the main eastern massif, at elevations between 3000-4050 m asl. *S. griseicauda* prefers bushy environments in the *Hericum-Hypericum* vegetation level (Rupp, 1980). and it is present in the Bale plateau as well as in Simien at about 3000 m (Yalden et al., 1976). However. it can be found also in more open habitats such as the prairies close to the Harenna forest (Yalden et al., 1996). This species replaces *M. albipes* over *3000* m and. in the Bale, it is replaced by *S. albocaudata* above 3500 m, at the *Erica arborea* zone.

Myomys, with its 7 species. is a widespread genus across Africa and as for many African genera, constitutes a taxonomic puzzle still deserving solution. *Myomys* is included in a group of genera with *Praomys*, *Mastomys*, *Hylomyscus*, and *Stenocephalemys*. However, the systematics and the definition of these genera are uncertain and some species of one genus may be more similar to species of another. This is the case of *Myomys fumatus*,

Table 1 – Species. number of individuals. latitude, longitude and altitude for the populations studied.

Species	Population	n. of individuals	Latitude	Longitude	Altitude
M. albipes	Addis Ababa	12	8°55'N	38°35'E	2800
	Goba	11	6°59'N	40°01'E	3000
	Dorse	X	6°14'N	37°34'E	2700
	Godare	11	7°26'N	35°00'E	810
	Sidamo	5	6°23'N	38°35'E	2650
M. ruppi	Bonke	3	6°11'N	36°31'E	3000
M. fumatus	Marsabit	7	2°18'N	37°54'E	1345
	Mt. Suswa	6	1°06'S	36°25'E	
S. albocaudata	Bale	21	7°06'N	39°47'E	3300-4100
S. griseicauda	Dinshu	22	7°06'N	39°47'E	3000-3600

Table 2 – Description of the landmarks (see Fig. 1).

	Landmark
1	Tip of the nasals at their anterior suture
2	Anterior medial point at tip of incisive foramina
3	Posterior end of each incisive foramen
4	Posterior end of the suture between palatine and maxillar
5	Posterior midline suture of palatines
6	Sphenoccipital suture
7	Anterior limit of the foramen magnum
8	Posterior limit of the foramen magnum
9	Lateral limit of the foramen magnum
10	Inner extreme curvature point of the zygomatic bar at the squamosus process
11	Maximal curvature on internal zygomatic bar
12	Inner extreme curvature point of the zygomatic bar at the maxillary process
13	Most anteirior point on the zygomatic spine
14	Infraorbital foramen (lower margin)
15	Anterior alveolar margin of first molar
16	Posterior margin of third molar
17	Anterior tip of the Eustachian tube
18	Anterior limit of external auditory meatus
19	Posterior limit of external auditory meatus
20	Midline intersection between nasals and frontals
21	Midline intersection between frontals and parietals
22	Midline intersection between parietals and interparietals
23	Tip of the occipital squama
24	Lateral margin of the parietal-interparietal suture
25	Posterior margin (external) of the zygomatic bar at the squamosus process
26	External posterior limit of the zygomatic bar at the squamosus process
27	Internal dorsal maximal curvature of the zygomatic bar
28	Infraorbital foramen (upper margin)
29	Lateral suture between maxilla and premaxilla
30	Lateral suture between premaxilla and nasal
31	Point on frontal at greatest interorbital constriction
32	Suture between frontal and parietals at the temporal line
33	Extreme curvature of the temporal line

which is more similar to *Mastomys natalensis* than to any other *Myomys* species, according to immunological and karyological data (Qumsiyeh et al., 1990).A recent analysis including cytogenetics and allozymes (Corti et al., 1999). as well as the mitochondrial 16S rRNA sequences (Fadda et al., submitted) did not reach a clear conclusion on the phylogenetic relationships between *Myomys* and *Stenocephalemys*.

The purpose of this work is to investigate the morphometric relationships between the four endemic Ethiopian species of the two genera (*S. albocaudata*, *S. griseicauda*, *M. albipes*, and *M. ruppi*) and to suggest possible explanations for the differences in size and shape, either as adaptations to their peculiar environments or as the result of shared common ancestry. *M. fumatus* has been included for comparison purposes, being considered the closest relative to this complex (Misonne, 1969).

The shape of the skulls was studied using three-dimensional (3D) landmarks. This allowed a description of actual three dimensional shape changes instead of the two dimensional approximate (2D) geometric morphometrics, or distance based "traditional morphometrics" (Marcus, 1990).

Skull variation was studied using a generalised Procrustes analysis (see Bookstein, 1996 for a review). This is equivalent to an analysis of the weight matrix including the uniform component using a Thin Plate Spline approach, but without the possibility of showing results as splines.

MATERIALS AND METHODS

One hundred and six individuals were studied, representing the five species (Tab. 1; Fig. 1). *M. albipes* is represented by seven populations occurring at different altitudes, between 800 m and 3000.

S. albocaudata and *S. griseicauda* were collected in the Bale massif, with the exception of one individual of *S. griseicauda* from Arussi. *M. ruppi* is represented by 3 individuals from Bonke, Gamu Gofa. The two populations of *M. fumatus* are from Kenya.

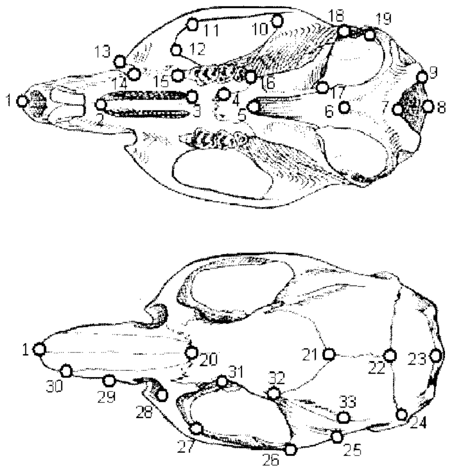

Figure 2 – **Skull** of *Stenocephalemys* with the location of the three-dimensional landmarks (see table 2).

The age of each specimen was estimated on the basis of molar toothwear, and 5 age classes were defined following Verheyen and Bracke (1964).

Specimens come from the permanent collections of the Museo di Anatomia Comparata, Universita' di Roma "La Sapienza"; Natural History Museum, London; Museum d'Histoire Naturelle de Paris; and Stuttgart Natural History Museum.

Thirty-three, 3D landmarks (Fig. 2: Tab. 2) were obtained for each skull through the procedure of Fadda et al. (1997).

Size was estimated as centroid size, the square root of the sum of the squares of the distances between each landmark and the centroid (Slice et al.. 1996). ANOVA was used to estimate differences in size among age classes for each species and among species and between sexes. *M. fumatus* and *M. ruppi* were excluded from the analysis of growth effects because of inadequate sample sizes. Differences in growth between species were tested through multiple comparisons of slopes. Finally, a partial least squares (PLS) analysis was performed to test whether size differences are related to elevation, latitude and longitude.

As the skull is symmetrical, the landmark coordinates of the two sides were averaged to avoid asymmetry and duplication of information. The values of the *y* co-ordinate of the landmarks situated on the sagittal plane were then set to 0. Therefore, data analyses were performed on one side of the skull only. but visualised using the reconstructed entire skull.

We superimposed and aligned the specimens to a consensus form using a Procrustes method corresponding to the 'partial Procrustes fitting' described by Dryden and Mardia (1998) and Rohlf (in press). The tangent space approximation to Kendall shape space was estimated by correlating the Procrustes and the Euclidean tangent space distances (Rohlf, 1998, Marcus et al., this volume).

After superimposition, Procrustes residuals were used for all further shape analyses. As the number of variables is large (the number of coordinates equals the number of landmarks multiplied by 3, i.e. 105) in comparison to sample size (110 specimens). we used a Principal Components Analysis to reduce dimensionality of the data. In order to identify a suitable number of principal components to retain for statistical estimates of shape changes, we correlated total Procrustes distance and the tangent space distances between specimens in PC space increasing the number of principal components until the correlation was large enough. The number of dimensions in shape space for a three dimensional data set is 3p-7

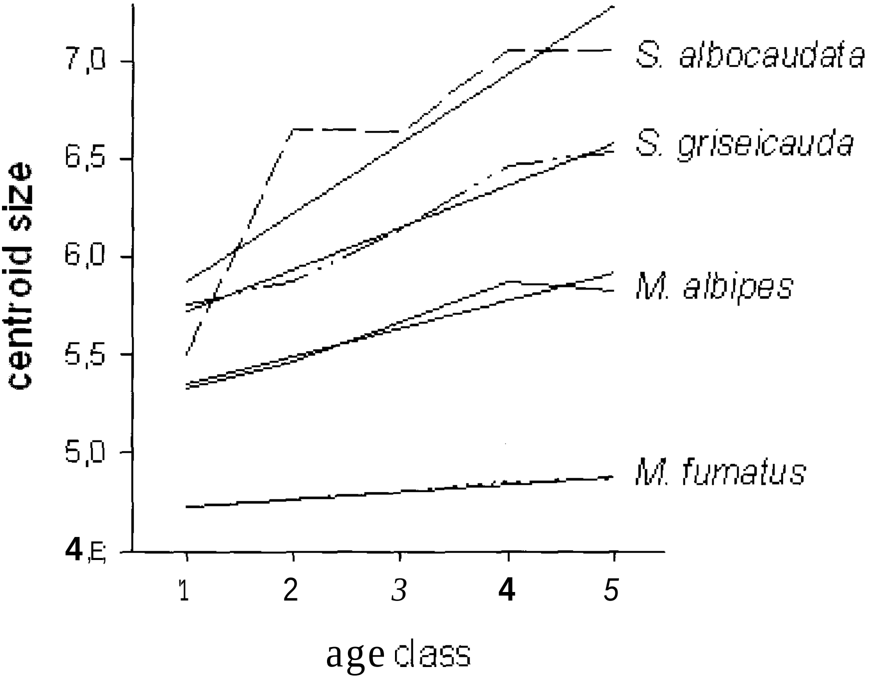

Figure 3 – Comparisons of mean centroid size for age stages between the species, from age class 1 to age class 5. Regression lines are superimposed on each species trajectory.

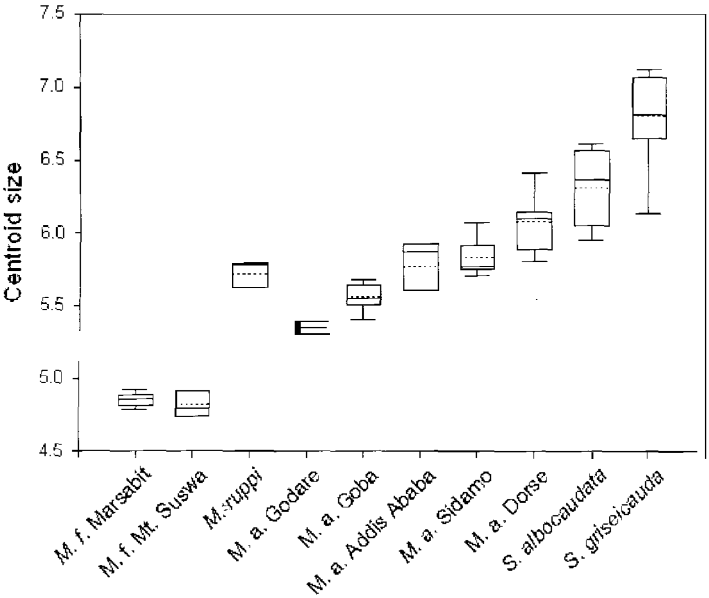

Figure 4 – Box plots for centroid sizes for populations. The dotted line represents the mean, the solid line the median, box margins at 25th and 75th percentiles. Bars extend to 5th and 95th percentiles. *M. a.* = *M. albipes*; *M. f.* = *M. fumatus*.

(Bookstein, 1996), where p is the number of landmarks (in our case (3*35)-7=98). Therefore, separate distance matrices were computed for the first to the 98th principal component. This procedure is a sort of inverted scree plot where the number of principal components to be retained is established choosing the high enough correlation coefficient, and reading off the chart the number of PCs to retain.

A MANOVA was performed on the selected principal components to estimate the overall shape differences between age classes, sex and species. An ANOVA was then performed on each separate principal component to dissect and test the sources of variation in relation to sex, age classes. and species.

The program GRF-nd was used for visualisation (Slice, 1992-94). by projecting selected eigenvector into the aligned co-ordinate system and plotting the individuals with the negative and positive coefficients.

The population and species were clustered as a UPGMA phenogram based on the Procrustes distances.

The pattern of covariation between shape variables (*S*, the selected principal components) and geographic variables (*G*, i.e. latitude, longitude and altitude) was explored by partial least squares (PLS; Streissguth et al. 1993).This technique finds relationships between the two sets of variables without being constrained by the necessity of orthogonality within each set as in canonical correlation analysis. PLS constructs pairs of vectors, to multiply by the columns of the *S* and *G* matrices respectively, which represent linear combinations of the variables within each set. These linear combinations are such that the constructed variables account for as much as possible of the covariation between the two original sets of variables. The new variables describe what patterns, if any, of covariation exist be-

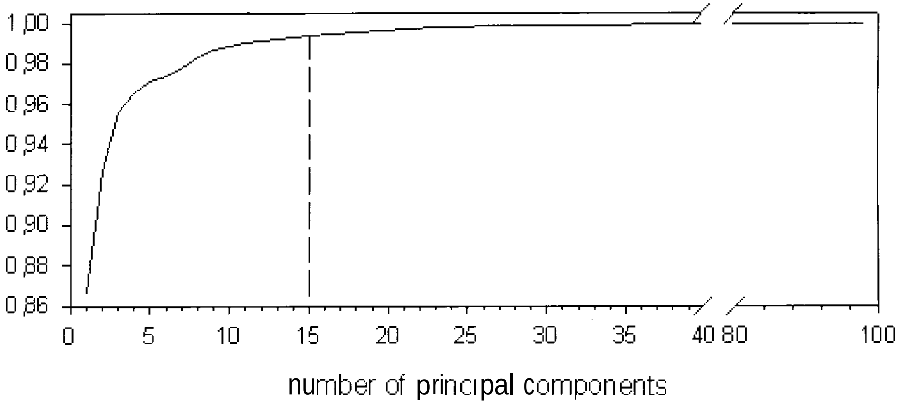

Figure 5 – Plot of the values of the correlation coefficient, *r*, between Procrustes distances and the Euclidean distances as a function of the number of principal components included, from 1 up to 98 PCs. The dashed line indicates the number of principal components (15, explaining 79.71% of the total variance, with ***r*** = 0.993) retained in the analysis of shape.

tween the two sets of original variables (see Rohlf and Corti, 2000).

All computations were performed using the **SAS** System for the PC **(SAS.** 1993) and the Beta version 2.01d of NTSYSpc (1996-1997)

RESULTS

Size. There is a significant "growth" effect in each species. Growth patterns are shown as curves in figure 3, which also include *M. fumatus*. The slopes are significant between *M. fumatus* and all other species, between *M. albipes* and all other species, and not significant between *S. griseicauda* and *S. albocaudata*. **No** sexual dimorphism in centroid size has been found for any species. Differencec between species are all significant for centroid size.

The summary for populations and species are shown as box plots in figure 4. *S. albocaudata* is the largest, followed by *S. griseicauda*. *M. fumatus* is the smallest, while *M. ruppi* and *M. albipes* are intermediate in size.

The multiple correlation coefficient between centroid size and latitude, longitude, and altitude was positive and significant. and the correlation with altitude was r=0.77.

Shape. The correlation coefficient between Procrustes and tangent space distances is very close to 1, suggesting that tangent space is an adequate approximation to Kendall

Table 3. Shape differences between species: ANOVAs for the first three principal components. Numbers indicate which PCs 1, 2, or 3 were significant for a specific comparison; n indicates none were significant. *Ma* = M. *albipes; Mf* = *M. fumatus; Mr* = *M. ruppi; Sa* = *S. albocaudata: Sg* = *S. griseicauda*

Species	*Mf*	*Mr*	*Sa*	*Sg*
Ma	2, 3	n	1	1
Mf		2	1, 2	1. 2, 3
Mr			1	1
Sa				1, 2, 3

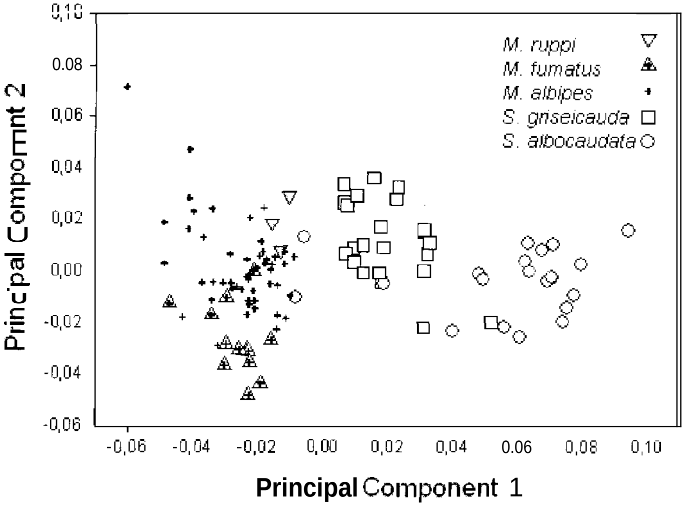

Figure 6 – Scatter plot of PC1 and PC2 scores.

shape space (see Marcus et al., this volume). Figure 5 shows the increase of correlation between total Procrustes distances and Euclidean distances as a function of the number of principal components included in the calculation. A sharp increase for the first few PC's begins to level off and then becomes asymptotic after 15 or more PC's. Therefore, further shape analysis was performed using the first 15 principal Components, explaining 79.71% of the total variance.

A MANOVA on the retained principal components indicates no effect due to sex and age for *Stenocephalemys* and *M. fumatus* and a slight significance for *M albipes*. Therefore, further analyses pooled individuals of different ages and sex.

Differences between species are highly significant (P<0.0001 according to Wilks' **A**). Hotelling T^2 tests showed that all paired differences between species are significant at P<0.01, after Bonferroni adjustment (Marcus, 1991; Morrison, 1976).

ANOVAs for the first. second, third, fifth, seventh, and thirteenth principal components are significant for species differences (Table 3). However, none of the individual principal components found significant differences between ***M.** alhipes* and *M. ruppi*.

The first principal component (36.2% of the total variance) shows a different ordination of the two genera *Myomys* and *Stenocephalemys*, with *S. griseicauda* having intermediate scores (Fig. 6). Shape differences associated with the first principal component are shown in figure 7. The main feature characterising *S. albocaudata* (positive scores) pertains to the braincase, the orbital region, and the rostrum. The former is shorter, due to a constriction of the parietals, interparietals and occipitals. and it is compressed dorso-ventrally. Interorbital constriction becomes narrower, the zygomathic arches expand laterally and the maxillary process of the jugal has moved upward, related to a modified position of the eyes.

It is interesting to note that shape differences between *M. albipes* and ***M.** fumatus* (second principal component, Fig. 7) are mainly represented by a dorso-ventral expansion of the entire skull in the latter. **As** a consequence, the dorsal profile of *M. fumatus* is much more convex, with the chondrocranium basis and the tympanic bullae moved downwards.

The UPGMA phenogram based on Pro-

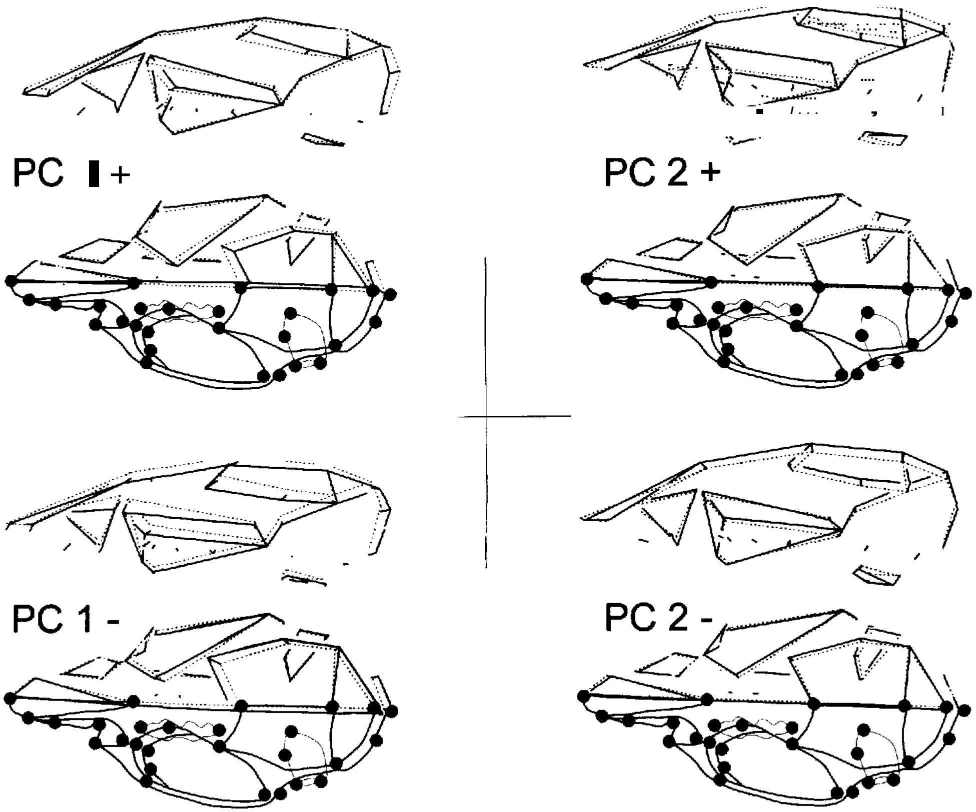

Figure 7 – Shape changes associated with the first two principal components. for the dorsal and the lateral views of the skull. On the left shape changes for the first eigenvector (PC 1): and on the right those for the second eigenvector (PC 2). The dotted lines represent the consensus. The plus and minus signs correspond to individuals with the highest and lowest scores for that vector (see Fig. 6): *S. albocaudata* (PC 1 +) and *Myomys* (PC 1 -); *M. albipes* (PC2 +) and *M. fumatus* (PC 2 -). Shape differences are magnified by a factor of 1.75

crustes distances (figure 8) clusters species in their respective genera. *M. ruppi* and *M. albipes* are much more similar than *S. griseicauda* and *S. albocaudata*.

The PLS analysis suggests a very close relationship between morphometrics and altitude. Correlation coefficients between variables and first vector in each of the two blocks (shape and geographic location) are as follows: first shape vector has a correlation of $r = 0.81$ with the first principal component, while altitude has a correlation of $r = 0.99$ with the first geographic vector (Fig. 9). These two vectors have a correlation of $r = 0.72$ and represent 71.3% of the total covariance. This result suggests that the pattern of shape differences observed in the first principal component can be interpreted as a result of adaptation to altitudinal variation (and, therefore, to the different environments characterising different elevations).

Discussion. Species can be recognised on the basis of skull size and shape. How much do site and shape changes reflect adaptation

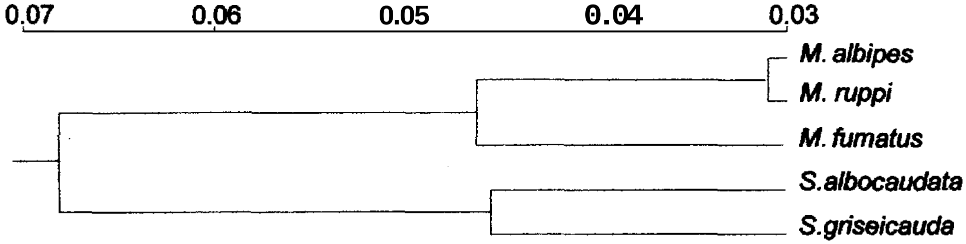

Figure 8 – UPGMA phenogram based on Procrustes distances between the species.

to the very different habitats? Or are rather consequences of divergence in isolation during and after cladogenesis?

Pleistocene rifting and climate fluctuations have increased habitat diversity. promoting divergence in East African species through shifts in ecology and geographic isolation. *Myomys* and *Stenocephalemys* presumably have been affected by these geo-climatic events.

Phylogeny inferred from part of the mitochondrial rRNA 16S gene (Fadda et al., in press) strongly suggests that *S. albocaudata* is the sister group of a clade including *S. griseicauda* and *M. albipes*. Moreover, it also shows that speciation within this group is very recent, as it occurred in the last 1.5 - 2 MY Bp. This result contradicts morphometric relationships and also phylogenies inferred from karyotypic rearrangements and electrophoresis (Corti et al.. 1999). However, maybe due to the short time of divergence, karyotype rearrangements and allozymes are much more ambiguous than DNA in depicting phylogenetic relationships. The morphometric relationships (as exemplified by the UPGMA in Fig. 8) can be interpreted as supporting the presence of two, separate monophyletic genera and agree with the accepted taxonomy. But. there is a strong suspicion that much of the size and shape changes occurred as adaptations to very different environments, so that shape characters are of little use for phylogenetic assessment.

Concerning size, growth curves are peculiar to each species: Not only are individuals at higher altitudes larger when young, they also grow at a proportionally faster rate. As shown in figure 3, there is a significant exaggeration in growth rate from lowlands to highlands, and this too supports the hypothesis of size increase as a clinal adaptation to altitude.

The fact that size is positively correlated with altitude (Fig. 4) can be interpreted as a realisation of Bergmann's rule, as already suggested by Rupp (1980). Studies on other Ethiopian rodent endemics did not show any increase in size with altitude, i.e. *Arvicanthis* (Afework Bekele et al., 1993; Corti and Fadda, 1996) and *Lophuromys* (Afework Bekele and Corti, 1994). Furthermore, Yalden and Largen (1992) showed that this is not a pattern common to other Ethiopian endemics (*Canis sinziensis, Capra walie, Crocidura. Tragelaphus buxtoni and Lepus starcki*).

Shape differences between species reflect the accepted taxonomy of the two genera. However, the strong relation with altitude shown by PLS (Fig. 9), suggests altitude as a plausible causal factor for shape changes. From the broad-leafed trees at 1000 m. vegetation composition progressively changes up the mountains, with successive zones of forest trees such as *Aningeria*, *Juniperus*, *Hagenia*, across the bushy *Erica* and *Philippia* belt, and up to the Afrolpine moorland occurring after the treeline, at about 3300 m (Yalden et al.. 1996).This al-

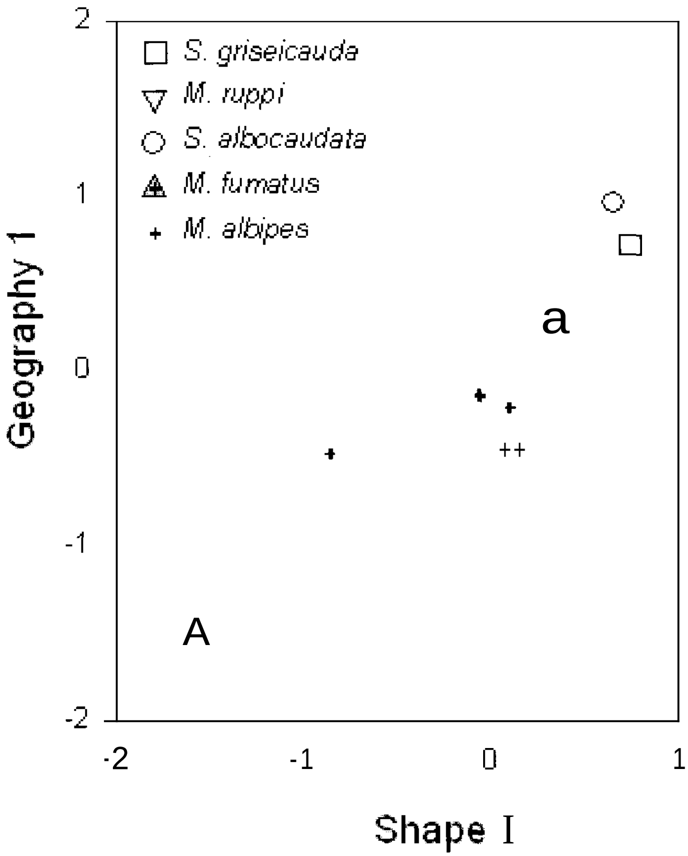

Figure 9 – Scatter plot of Partial Least Square of the first latent shape and geography vectors.

titudinal change in vegetation is accompanied by an evident process of stenocephaly (i.e. restriction of the inter-orbital width) and an enlargement of the zygomathic arches (previously discussed by Petter, 1972), which do represent an adaptation to progressively more open habitats characterising high altitudes. Stenocephaly is an advantage in an open country environment. such as grasslands and the **Afro** Alpine moorlands of the Bale, as it can scan the sky more efficiently for birds of prey. These are the main category of predators together with the Simien wolf (Yalden and Largen, 1992).

There is one final consideration concerning *M. ruppi*. Van der Straeten and Dieterlen (1983) established the species on the basis of traditional morphometrics by comparing several species of *Myomys* and *Stenocephalemys*, and including in the analysis the seven specimens from Bonke *(M. ruppi)* using canonical variates. These had scores in between the former two, with a closer relationship to *S. griseicauda*. This was considered sufficient to define the Bonke population as a separate and new species, *M. ruppi*. However. our geometric morphometrics analysis does not support their conclusion, as *M. ruppi* shares centroid size values and shape changes that are typical of *M. albipes* (Tab. 3). There are obvious limitations due to the limited number of individuals in the present analysis as well as in that of Van der Straeten and Dieterlen (1983). Nonetheless, there is evidence (Fadda et al., in press) suggesting a process of divergence within Ethiopian *Myomys*, so that the taxonomic status of the Bonke population, as well as for other populations, still remains open.

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