Hystrix, (n.s.) 11 (1) (2000): 145-154

THREE-DIMENSIONAL GEOMETRIC MORPHOMETRICS OF THE AFRICAN GENUS *LOPHUROMYS* (RODENTA MURIDAE).

MARCO CORTI (*), CRISTIANA DI GIULIOMARIA (*)
AND WALTER VERHEYEN (**)

(*) *Dipartimento di Biologia Animale e dell'Uomo, Università di Roma "La Sapienza",*
via Borelli 50, 00161 Roma, Italy; e-mail. marco.corti@uniroma1.it
(**) Department of Biology, Groenenborgerlaan 171, 2020 Antwerp, Belgium

ABSTRACT - Three-dimensional geometric morphometrics was used to investigate patterns of growth and differences in size and shape of the skull of three species of the African rodent genus *Lophuromys*, representing the two subgenera *Lophuromys* s.s. (represented by a population of *L. flavopunctatus* from Rwanda and a population of *L. sikapusi* from Ivory Coast) and *Kivumys* (represented by a population of *L. woosnami* from Rwanda). Procrustes superimposition was used to study variation in 21 three-dimensional landmarks. Differences in shape were visualised by using current available graphical morphometric techniques. Significant differences in centroid size were found both between species, sexes, and age classes. The pattern of growth in size is parallel between species. suggesting that it has been maintained after cladogenesis. No significant sexual dimorphism in shape has been found. Moreover. growth significantly affects the shape of the skull of *L. flavopunctatus*, but not that of *L. sikapusi* and *L. woosnami*. The main distinction in shape reflects the phylogenetic occurrence of the two subgenera, i.e. *Kivumis* and *Lophuromys* s.s. However, the knowledge on the biology of these species is inadequate to exclude that any other adaptive factor (e.g. diet, climate, etc.) may have contributed in causing shape differences.

Key Words: Lophuromys, African Rodents, Geometric Morphometrics, Procrustes analysis, 3-D morphometrics.

INTRODUCTION

Application of three-dimensional geometric morphometrics in mammalogy is relatively unexplored. However, three dimensional skeletal structures such as the skull, have been the primary source of distance measurements in traditional morphometrics (Marcus, 1990). The skull contains the brain, the major sensory organs, the feeding apparatus, and it also contains a lot of information on the ontogeny, phylogeny, and adaptation. Thus, it is not surprising that it has been the main source for characters.

Since the origin of geometric morphometrics, most applications in mammalogy dealt with two-dimensional representations of the skull, digitised as images of the dorsal and ventral sides, which were usually analysed separately (e.g. Loy et al., 1993; Bogdanowicz and Owen, 1996; Corti and Fadda, 1996; Rohlf et al., 1996). Attempts to find patterns of co-variation in shape changes between the different skull views have been made only a-posteriori (see Corti and Rohlf, submitted).

Few papers have dealt with three-dimensional geometric morphometrics of small mam-

Table 1 – Species, locality, age class, and the number of individuals (first rows are males, second rows females) for each age class.

Species	Locality	**age** class					Subtotal	**Total**
		0	**1**	**2**	**3**	**4**		
L. flavopunctatus (Rwanda)	Mutura	8	7	7	6	4	32	58
		2	5	5	6	8	26	
L. sikapusi (Ivory Coast)	Mopoyem	-	7	10	8	9	34	*63*
		-	10	11	7	1	29	
L. woosnami (Rwanda)	various	1	-	7	6	10	24	51
	lacalities	3	-	6	11	7	27	51

mals (Corti et al.. 1996; Reig, **1996;** Fadda et al.. 1997; Fadda. 1998). It has been difficult or required expensive equipment (Reflex microscope for example, Dean, 1996) to collect 3-D landmarks on small objects, such as rat and mice skulls. There are also some methodological limitations in the theory (e.g. the lack of a formula to compute the uniform transformation), and visualisation and presentation of results (but see the programs Morpheus et al. by Slice, 1994-98; and Morphologika by O'Higgins and Jones, 1998).

In this paper we present a case study of a three-dimensional morphometric analysis of the skull of three species of African rodents of the genus *Lophuromys* Peters, 1874. We used Procrustes superimposition to investigate patterns of growth and species differences in both size and in shape. We also tried to visualise these patterns through an integration of available graphical techniques.

Lophuromys is a widespread genus through all tropical Africa, with many species in a variety of environments and altitudes. The genus is peculiar among rodents, being that **the diet is** specialised for eating insects (Dieterlen, 1974). A revision of the genus has proposed a division into the two subgenera *Lophuromys* Peters 1874 and *Kivumys* Dieterlen 1987 (Dieterlen, 1987). The three species studied here, *L. sikapusi*, *L. flavopunctatus*, and **L.** *woosnami*, are the most common and best known. The first two species are included in the subgenus *Lophuromys* s.~., and the latter in the subgenus *Kivumys*. The range of the ***L. sikapusi*** species group extends from Sierra Leone, to Zaire. Uganda, West Kenya and North Angola. The *L. flavopunctatus* species group occurs from Northwest Angola, across Zaire. Uganda, Kenya. Ethiopia. Sudan and Tanzania up to Malawi, Northern Zambia and Mozambique. *L. woosnami* has a smaller range. limited to Rwanda, Burundi, Eastern Zaire and West Uganda.

MATERIAL AND METHODS

A hundred and eighty-five specimens representing the three species (Tab. 1) were studied. *L. flavopunctatus* and *L. sikapusi* come from single localities in Rwanda (Mutura; 1" 26' S, 30" 28' E; 1480 m asl) and Ivory Coast (Mopoyem; 5° 18' N, 4" 27' W; 0-100 m asl), respectively. Specimens of *L. woosnami* were collected from eight different localities in Rwanda, which were pooled together in **the** analyses. **At** one **of** these localities, **Mutura,** the species occurs in sympatry **with** ***L. flavopunctatus.***

Age class was determined on the basis of **molar** tooth-wear. from 0 **up** to 4 following Verheyen et *al.* (1996).

Images of individuals were digitised **using** a Canon E700 camera and an OFG digitising hoard **(VP** 1100-512-U-AT), with a resolution of 512 by 480 pixels. Six images were recorded by rotating the skull of each indi-

Figure 1. Skull of *Lophuromys* with the location of the 21 three dimensional x, y, z landmarks (see table2).

vidual at different angles, i.e. 0" (ventral side), 45°, 120°, 180° (dorsal side), 240°, and 315°, using the device described in Fadda et al. (1997). Two-dimensional, x,y landmarks were then collected on each of these images (19, 11, 10, 15, 10, 11, respectively) using the software TPSDIGW (Rohlf. 1996). The six arrays of landmarks were translated to a common origin (landmark 1), with landmarks 1, 2, 3, 4, 5, 13, 14, and 15 (sagittal section) defining the x, y plane. Each array was then rotated around the x-axis (landmarks 1 and 5) by the number of degrees at which each image was recorded. The values of the 21 x, y, z three-dimensional landmarks were then obtained following the algorithm described in Fadda et al. (1997).

A description of the 21 landmarks is given in table 2 and figure 1.

Lateral asymmetry was removed from the data by averaging the values of the landmarks on the left and right sides of the skull and then setting the y co-ordinate to 0 for the landmarks in the sagittal plane.

Size was estimated as centroid size (Slice et al., 1996), and used to investigate size differences between sexes, age classes and species. The three-dimensional co-ordinates were translated, scaled through the 'partial Procrustes fitting' (Dryden and Mardia, 1998), and fit by the Procrustes Generalised Least Squares method. The Procrustes co-ordinates of one side of the skull (21 landmarks) were then used in all analyses, and the whole view was used for visualisation.

Correlation between the Procrustes (shape space) and the Euclidean (tangent space) distances was checked by correlating the distance matrices to assess the approximation of tangent space to shape space.

Principal components of Procrustes residuals were used to investigate shape differences. **P** - 7 (56) eigenvectors were examined, where P is the number of landmarks multiplied by three. The last seven eigenvectors represent scaling (one parameter), translation and rotation (three parameters each), and therefore were discarded (Bookstein, 1996). In order to reduce the dimensionality of the data. all statistics were performed on the scores of the first ten principal components, representing 88.5% of total variance (see Fadda and Corti, this volume). Tests for differences in age. sex. age-by-sex

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

n°	Landmark
1	Tip of the nasals at their anterior suture
2	Anterior end of the incisive foramina
3	Posterior end of the incisive foramina
4	Posterior end of the suture of the palatines
5	Anterior limit of the foramen magnum
6	Lateral limit of the foramen magnum
7	Tip of the auditory meatus
8	Petrotympanic fissure
9	Tip of zygomatic plate
10	Anterior margin of first molar alveolus
11	Posterior margin of third molar alveolus
12	Tip of the Eustachian tube
13	Sagittal suture between frontals and nasals
14	Sagittal suture between frontals and parietals
15	Sagittal suture between parietals and interparietal
16	Sagittal tip of the lambdoidal crest
17	Intersection between temporal and lamboid sutures
18	Posterior inferior tip of squamosal root of zygomatic bar
19	Temporal line at the frontal - parietal suture
20	Upper end of infraorbital foramen
21	Lower end of infraorbital foramen

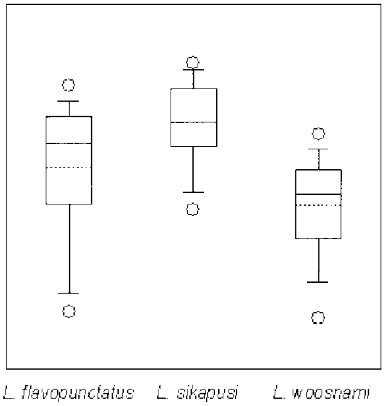

Figure 2. Box plots of centroid size for the three species of *Lophuromys*. The solid line is the median and the dotted line is the mean. Box margins are at 25th and 75th percentiles: bars extend to 5th and 95th percentiles: and circles are at the smallest and largest values.

interaction, and species were based on scores of these ten principal components using ANOVA and MANOVA.

We used integrated graphical representations obtained from GRF-ND (Slice, 1992-94), Morpheus et al. (Slice, 1994-1998), and, for three-dimensional surface rendering. Geomagic Wrap (1998, version 2.1). In order to produce more satisfactory visualisations. shape changes associated with principal components were exaggerated by a factor of 4. A routine written in Matlab by X. Penin was used to compute the eigenvectors and to exaggerate the extreme (positive and negative) individuals on each axis.

SAS (1993) was used for all statistical analyses and for 3D landmark reconstruction from 2D images, following the routine of Fadda (1998). The programs GRF-ND (Slice, 1992-94) and Morpheus et al. (Slice, 1994-98) were used to extract centroid size, and for Procrustes fitting (from the Stony Brook WWW morphometric site at http://life.bio.sunysb.edu/morph).

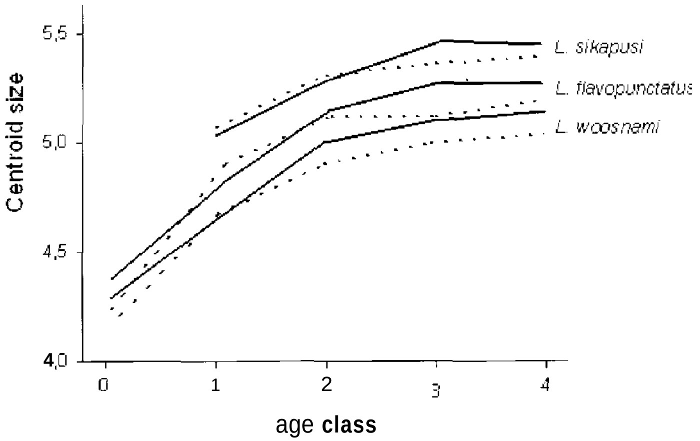

Figure 3. Comparisons of mean growth in size among the species from age class 0 to age class 4, separately for the two sexes. The solid lines are for males and the dotted lines for females.

RESULTS

Size. There are always significant differences in centroid size between age classes in each species. Centroid size is also a sexually dimorphic character in *L. flavopunctatus* (age classes 0 and 3) and *L. woosnami* (age classes 2, 3, and 4), but not in *L. sikapusi.*

Centroid size comparisons between species are represented by box plots in figure 2 (juveniles excluded). *L. sikapusi* is the biggest, and *L. woosnami* the smallest, with ANOVA significant differences (F= 102.35, d.f. 2, 180; P<.0001).

The comparison of the increase in size between species during growth is shown in figure 3, separately for the two sexes, and it suggests that although species differ in size. they keep a common and parallel pattern. Moreover, females at age class 0 are smaller in size than males. but at age class 1 they become larger. From age class 2 up to age class 4 males become larger.

Shape. The approximation of shape space by the tangent space was almost perfect (the correlation between Procrustes and Euclidean distances was 1 to 5 decimal places), making all statistical estimates of shape differences extremely reliable. As expected. variation in shape occupies only a small fraction of shape space (cfr. Marcus et al., this volume).

Separate MANOVAs for each of the three species evidenced that there is no significant sexual dimorphism in shape. Mcreover, the shapes of the skulls of *L. sikapusi* and *L. woosnami* do not change significantly during growth. On the contrary. *L. flavopunctatus* exhibits a clear and significant distinction between age classes (P<.005 according to Wilk's **Λ).**

This is reported in fig. 4, where the first principal component (23.1% of variance) clearly represents a growth vector where individuals are ordered according to their age class. An ANOVA run on this first PC shows that differences between age classes are highly significant (F=29.6; d.f. 4. 53: P<.0001).

Shape changes associated with this growth vector are represented in fig. 4. The rostrum gets progressively thinner as the animal grows, especially at the insertion of the zygomatic bar, with a reduction of the parietals and interparietals. a typical pattern in mammals. Thin plate-spline grids in frontal and transverse sections suggest that this is accompanied by a progressive extension forward of the nasals and frontals, relatively to the palate, i.e. the molar toothrow does not accompany this shift.

A MANOVA run on the 10 principal components of the Procrustes aligned specimens showed that there is a significant interaction between age and species (P<.0001 according to Wilk's **A**).

A MANOVA excluding age classes 0 and 1 did not show any significant difference between sexes, age classes, and no significant interaction between these and species. There was only a highly significant difference between species (P<.0001 according to Wilk's **A**, Pillai's Trace, Hotelling, and Roy's greatest root). The Hotelling's T^2 test shows that all pairwise species differences (after Bonferroni adjustment) are significant at P<.001. The first two principal components account for 41.66% of total variance (28.54% and 13.11%, respectively). The first eigenvector express differences in shape between *L. woosnami* (lowest scores), and *L. flavopunctutus* and *L. sikapusi* (highest scores) (Fig. 5). The second eigenvector represents differ-

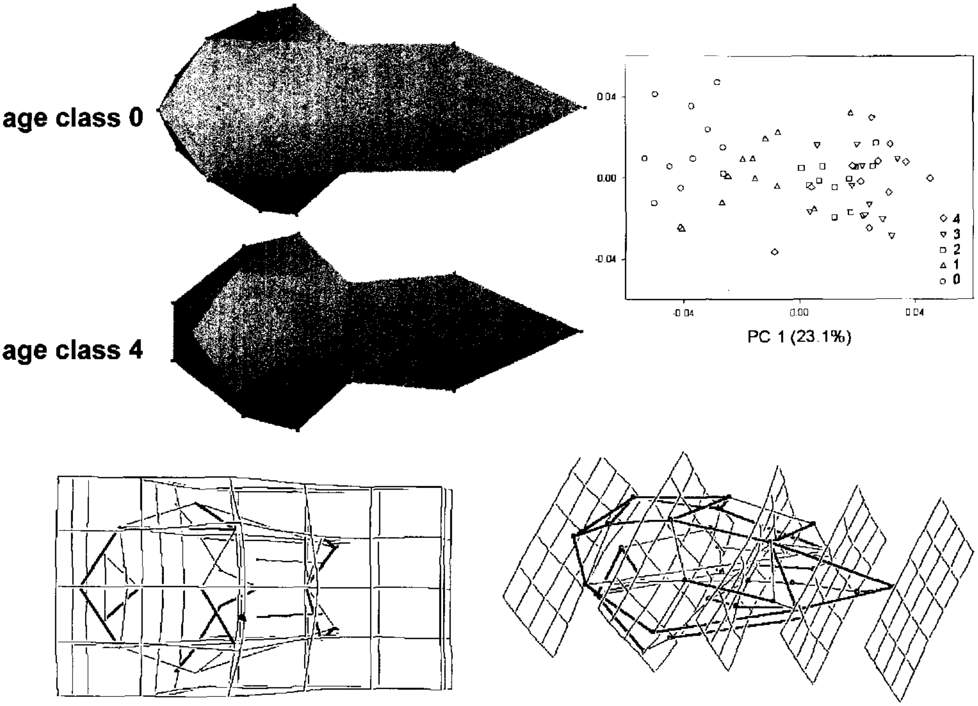

Figure 4. Shape changes during growth in *L. flavopunctatus*. Upper right: PC 1 vs. PC 2 scatter plot is reported, showing an ordination (PCI) of age classes from 0 to 4. Shape changes corresponding to PC 1 are represented as a dorsal side three-dimensional surface reconstruction.
Three dimensional representations with links connecting the landmarks and thin plate-spline grids (transformation from the juvenile to the adult class) are represented in the bottom part of the figure. Bottom left: dorsal view with grids in the frontal planes; bottom right: lateral view with grids in the transverse planes. Shape changes have been intentionally exaggerated by a factor of 4.

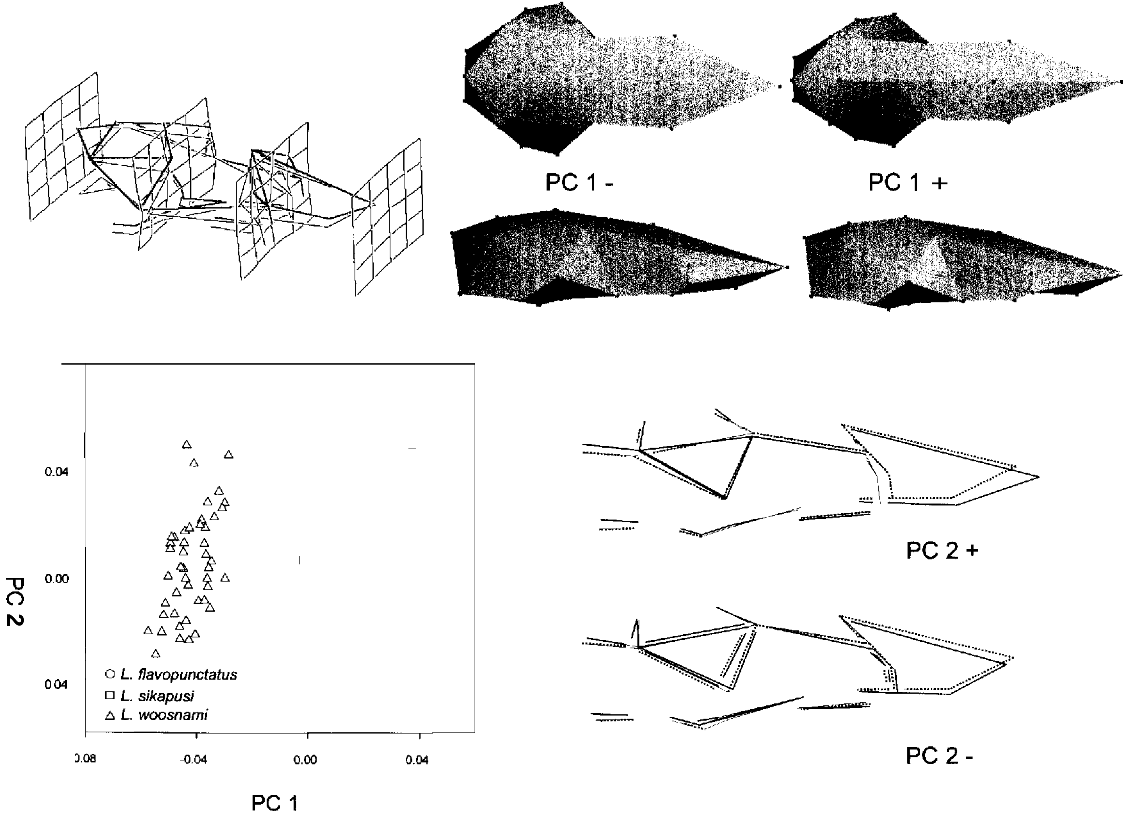

Figure 5. Shape changes between the three species of *Lophuromys*. Lower left corner: PC 1 vs. PC 2 scatter plot. Upper right corner shows shapes as lateral and dorsal three-dimensional surface reconstruction of the skull for the highest (PC 1 +, *L. sikapusi* and *L. flavopunctatus*) and lowest (PC 1 – , *L. woosnami*) values of PC1; Upper left corner: the same kind of shape difference is represented as a 3-D reconstruction with links connecting the landmarks and spline grids in the transverse planes (transformation of *woosnami* into *sikapusi*). Lower right corner: shape differences (solid lines) from the consensus (dotted lines) in the lateral view along PC 2: *L. flavopunctatus* (PC 2 -) and *L. sikapusi* (PC 2 +), respectively. Shape changes have been intentionally exaggerated by a factor of 4.

ences between *L. flavopunctatus* (lowest scores) and *L. sikapusi* (highest scores). Ordination of specimens onto these two PCAs has been tested by ANOVA, with highly significant differences (F=646.1 and 14.58; d.f. 3, 125; P<.0001, for PC1 and PC 2 respectively).

The main shape changes between the *Kivumys* and *Lophuromys* s.s. groups concern the rostrum, which is shorter and larger in the former, and the palate, which, in *Kivumys* is higher and convex with respect to the molars. This is represented by the three dimensional reconstruction with rendering as dorsal and lateral views in Fig. 5. This pattern can be further appreciated by the thin plate-spline grids in frontal planes. Moreover, the braincase of *Lophuromys* s.s. is thinner and the parietals and interparietals are extended backwards.

The long rostrum characterising the *Lophuromys* s.s. group is even longer in *L. sikapusi* than in *L. flavopunctatus*, as highlighted by the second principal component (Fig. 5).

DISCUSSION

There is no doubt that these three species of *Lophuromys* are distinct in their size and shape. Main differences in shape reflect the phylogenetic occurrence of two separate subgenera, i.e. *Kivumys* and *Lophuromys* s.s., as reported by PC 1 (Fig. 5). As a result of the intense ecological and biological research efforts of Dieterlen (1976), the rodent genus *Lophuromys* is till now among the best documented African rodents. It was Dieterlen (1967) who described the new subgenus *Kivumys* comprising among others the species *L. woosnami* Thomas 1906. His decision to recognise the new taxon was mainly triggered by a set of comparative electrophoretic data published by Verheyen et al. (1986).

When we try to relate the observed morphometric differences to what is known of the ecology and biology of the studied species (Dieterlen. 1976), we come to the conclusion that geographic, climatological, habitat, reproductive and locomotory components can be safely excluded as causal factors for these differences.

Differences in size between species are significant, and size change across ages for the two sexes tends to keep the same pattern in the three species (Fig. 3), and the pattern has been presumably maintained through and after cladogenesis.

Concerning shape, there are however certain characteristics of diet and food processing that could be responsible for the observed differences. Indeed, the genus is characterised by a strong tendency to insectivory and some species are known to eat molluscs, annelids and even frogs (Dieterlen, 1976, 1987). This diet is directly reflected in the length of the digestive tract which is, when compared to other African Murids, very short (Dieterlen. 1976). When comparing representatives of the subgenus *Kivumys* to *Lophuromys* s.s. there are strong indications that the former are clearly more insectivorous than the latter. This is suggested by the fact that in *L. woosnami* 1) the length of the digestive tract is clearly shorter; 2) the cuspidation of the molars is clearly more pointed and sharper; 3) the form of the zygomatic arches and zygomatic plates arc weaker and more slenderly built indicating a weaker jaw musculature; and 4) the overall morphology of the mandible is more slender and delicate.

It is noteworthy that size but not shape is the only sexually dimorphic character. This fact however is not surprising at all, as all geometric morphometric analyses performed so far on Rodents and that partitioned size and shape have shown the same result (for *Arvicanthis* see Corti and Fadda, 1996. and Fadda, 1998; for *Myomys* and *Stenocephalemys*, Fadda, 1998, and Fadda and Corti, this volume; for *Spalax ehrenbergi*, Corti et al.. 1996; for *Calomys*, Hingst et al.. this volume: for *Mus*, Corti and Rohlf, submitted). Obviously, soft tissues are not included in our analysis, but it is interesting to note that shape changes – at least for the skull – are not involved in sexual dimorphism, even though the species (*L. flavopunctatus*) is characterised by territorial behaviour and social aggression.

Visualisation and discussion of shape changes using three-dimensional reconstructions is difficult. It is hard to produce the three-dimensional adjustments made by the human visual system using two-dimensional grids; — and to interpret covariation of landmarks in different areas that change their shape together, rather than to focus on one or two landmarks. Furthermore, differences in size and shape of structures with a strong three-dimensionality, such as the mammalian skull. can be perturbed by a two-dimensional approach. For example, Fadda (1998) compared three and two-dimensional analyses of the same data set through a Mantel plot and showed that Procrustes distances are larger in three dimensions than in two dimensions. Therefore. we are concerned that the reduction of three-dimensional biological forms to a *x*, *y* dimensional landmark representations may constitute an important problem. Further development of three dimensional analysis and visualization tools is needed.

ACKNOWLEDGEMENTS

We thank Xavier Penin for helping us to write and test a Matlab routine for visualisation of 3D displacements. This work was supported by grant Fondi 60% Facoltà "Sviluppo e sperimentazione di metodologie numeriche per lo studio della forma nelle 2 e 3 dimensioni", "Caratterizzazione della biodiversità in ambiente tropicale: un'analisi genetica, molecolare e morfometrica in Vertebrati", Fondi Ateneo cx – 60%. and "Commissione per i Musei Naturalistici dell'Accademia Nazionale dei Lincei".

REFERENCES

Bogdanowicz, W. and Owen, R.D., 1996. Landmark-based size and shape analysis in systematics of the Plecotine Bats. In: Marcus L.F., Corti, M., Loy. A.. Naylor. G. and Slice, D. (eds.), "Advances in morphometrics". Plenum Press. NY: 489-501.

Bookstein. F.L.. 1996. Combining the tools of geometric morphometrics. In: Marcus L.F., Corti, M., Loy, A., Naylor, G. and Slice, D. (eds.). "Advances in morphometrics". Plenum Press, NY: 131-151.

Corti, M. and Fadda. C., 1996. Systematics of *Arvicanthis* (Rodentia, Muridae) from the Horn of Africa: a geometric morphometrics evaluation. Ital. J. Zool., 63: 185-192.

Corti, M.. Fadda, C.. Simson, S. and Nevo, E., 1996. Size and shape variation in the mandible of the fossorial rodent *Spalax ehrenbergi*. In: Marcus L.F., Corti, M.. Loy. A., Naylor, G. and Slice, D. (eds.). "Advances in morphometrics". Plenum Press. NY: 303-320.

Corti, M. and Rohlf, F.J. Chromosomal speciation and phenotypic evolution in the house mouse. Submitted.

Dean, D. 1996. Three-dimensionan data capture and visualisation. In: Marcus L.F., Corti, M., Loy, A., Naylor, G. and Slice, D. (eds.), "Advances in morphometrics". Plenum Press, NY 53-69.

Dieterlen, F.. 1976. Die Afrikanische Muridengattung Lophuromys Peters. 1874. Stuttgarter Beitrage zur Naturkunde. 285: 1-96.

Dieterlen, F.. 1987. Neue Erkenntnisse über afrikanische Bürstenhaarmäuse, Gattung Lophuromys (Muridae; Rodentia). Bonn. Zool. Beitr., 38: 183-194.

Dryden, I. L., and Mardia. K. V., 1993. Multivariate shape analysis. Sankhya, 55:460-480.

Fadda, C., 1998. Sistematica e variazione geografica in roditori africani. Morfometria geometrica e filogenesi molecolare. PhD dissertation, Università di Roma "La Sapienza", 159 pp

Fadda. C.. Faggiani, F. and Corti, M.. 1997. A portable device for three dimensional landmark collection of skeletal elements of small mammals. Mammalia, 61: 622-627.

Fadda, C. and Corti, M., 2000 Three Dimensional Geometric Morphometric study of the Ethiopian *Myomys – Stenocephalemys* complex (Murinae, Rodentia). It. J. Mamm. (Hystrix) 11: 131-143.

Geomagic Wrap, 1998. Wrap, ver. 2.1. Raindrop Geomagic Inc., Champaign, IL.

Hingst-Zaher, E., Marcus, L.F. and Cerqueira. R., 2000 Application of geometric morphometrics to postnatal size and shape changes in the skull of *Calomys expulsus*. It. J. Mamm. (Hystrix). 11: 99-113.

Loy, A., Corti, M. and Marcus, L.F., 1993. Landmark data: Size and shape analysis in systematics. A case study on Old World Talpidae (Mammalia, Insectivora). In: Marcus. L.F., Bello, E., Garcia-Valdecasas, A. (eds.), "Contributions to morphometrics", Vol. 8, Museum Nacional de Ciencias Naturales, Madrid: 215-240.

Marcus, L. F., Hingst-Zaher, E. and Zaher. H., 2000 Application of Landmark Morphometrics to Skulls Representing the Orders of Living Mammals. It. J. Mamm. (Hystrix) 11: 27-47.

O'Higgins, P. and Jones, N. ,1998. Morphologika. University College, London,

Rahm, U., 1967. Les Murides des environs du Lac Kivu et des régions voisines (Afrique Centrale) et leur écologie. Rev. Suisse Zool., 74: 439-519.

Reig, S., 1996. Correspondence between landmark distances and caliper measurements. In: Marcus L.F., Corti, M., Loy, A.. Naylor, G. and Slice, D. (eds.), "Advances in morphometrics". Plenum Press, N Y 371-385.

Rohlf, F.J., 1996. TpsDig. Department of Ecology and Evolution, SUNY, N.Y.

Rohlf, F.J., Loy. **A.**, and Corti. M., 1996. Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial warp scores. Syst. Biol., 45: 344-362.

SAS, 1993. Statistical Analysis Software. Release 6.12. SAS Institute Inc. Cary, North Carolina

Slice, D.E., 1992-94. GRF-ND. Generalized rotational fitting of n-dimensional landmark data. Department of Ecology and Evolution, SUNY, N.Y.

Slice, D.E., 1994-98. Morpheus et al. Department of Ecology and Evolution, SUNY, N.Y.

Slice, D.E., Bookstein, F.L., Marcus, L.F. and Rohlf, F.J., 1996. A glossary for geometric morphometrics. In: Marcus L.F., Corti, M.. Loy, A., Naylor, G. and Slice, D. (eds.), "Advances in morphometrics". Plenum Press, N Y 531-551

Verheyen, W.N. and Bracke, E., 1964. The influence of aging in the craniometrical characters of *Praomys jacksoni* (De Winton, 1897). Ann. Mus. Roy. Afr. Centr., 8 Zool., 144: 91-110.

Verheyen, W., Michielis, M. and van Rompaey, J., 1986. Genetic differences between Lophuromys flavopunctatus Thomas, 1888 and Lophuromys woosnami Thomas. 1906 in Rwanda (Rodentia: Muridae). Cimbebasia, 8: 141-145.

Verheyen, W.N., Colyn, M. and Hulselmans, J.. 1996. Revalutation of the *Lophuromys nudicaudus* Heller, 1911 species complex with a description of a new species from Zaire (Muridae-Rdentia). Bull. Inst. Roy. Sci. Nat. Belgique, Biologie, 66: 241-273.