Biogeographia – The Journal of Integrative Biogeography

Title

A contribution to the phylogeny of the elephant shrews (Mammalia, Macroscelidea)

Journal

Biogeographia – The Journal of Integrative Biogeography, 29(1)

ISSN

1594-7629

Authors

Scalici, Massimiliano
Panchetti, Fabiana
Carpaneto, Giuseppe M.
et al.

Publication Date

2008

DOI

10.21426/B629110001

Peer reviewed

Biogeographia vol. XXIX - 2008
(Pubblicato il 30 dicembre 2008)
The Mediterranean-southern African disjunct
distribution pattern

A contribution to phylogeny of the elephant shrews (Mammalia, Macroscelidea)

MASSIMILIANO SCALICI, FABIANA PANCHETTI, GIUSEPPE MARIA CARPANETO, GIANCARLO GIBERTINI
Dipartimento di Biologia e Biologia Ambientale, Università Roma Tre,
via G. Marconi 446, 00146 Roma, Italy
e-mail: scalici@uniroma3.it; fabiana.panchetti@hotmail.it; carpanet@uniroma3.it; gibertin@uniroma3.it

Key words: geometric morphometric analysis, systematics, biogeography, Afrotropical Region

SUMMARY

The main purpose of the present study was to contribute to the systematic debate on the elephant-shrews, an order of mammals endemic to Africa, by comparing biogeographical patterns with the results of the analysis of cranium images using a geometric morphometric approach. A total of 529 images of dorsal and lateral crania of adult specimens belonging to all the living genera and 13 species were analyzed. The cranial features that distinguished the subfamily Rhynchocyoninae (*Rhynchocyon)* were a consequence of the extreme enlargement of frontal bones. Instead, within the subfamily Macroscelidinae (*Macroscelides, Elephantulus, Petrodromus*), the differences between genera were based on modification involving other bones, mainly mastoids and nasals, as shown by the deformation grids. A cluster analysis confirmed the traditional subdivision in the two subfamilies, but suggested a different relationship among the recognized genera belonging to Macroscelidinae. Our results also support the monophily of the genus *Elephantulus* and its closeness with *Petrodromus*, relating to their similar cranium shapes. The latter presumably is a case of gigantism as adaptation to forest habitats. Subsequently, the adaptative radiation of *Elephantulus* drove the savannas-dwelling species. We retain that the separation of *P. tetradactylus* and *E. rozeti* from their common ancestor could have occurred before the splitting of the other *Elephantulus* species, conserving some plesiomorphies in the cranium of these two species. The colonization of NW Africa by *E. rozeti* is the result of a vicariant event in which the Sahara desertification was instrumental. Further studies on all the species of *Elephantulus* could provide new evidence for assessing the relationships within this clade, including *Macroscelides* that appeared as a well-distinguished taxonomic entity.

INTRODUCTION

Living elephant shrews are an African endemic order, mouse-like in appearance, small-bodied, cursorial and saltatorial, insectivorous and omnivorous, placental mammals (Corbet & Hanks, 1968; Kingdon, 1974; Rathbun, 1979). Elephant shrews originated from Africa and never spread out of this continent (Patterson, 1965). Recent molecular studies of mammalian phylogeny evidenced that this clade belong to Afrotheria, the latter also involving elephants, sea cows, hyraxes, aardvark, golden moles and tenrecs (see Springer et al., 1997; Stanhope et al., 1998; Seiffert, 2008). All the living elephant shrews belong to the same family Macroscelididae (Patterson, 1965; Corbet & Hanks, 1968; Corbet, 1974; Schlitter, 1993), involving four genera and 16 living species, separated into the two subfamilies Rhynchocyoninae (*Rhynchocyon* Peters, 1847: 4 species) and Macroscelidinae (*Macroscelides* Smith, 1821: 1 species; *Petrodromus* Peters, 1846: 1 species; *Elephantulus* Thomas & Schwann, 1906: 10 species). *Macroscelides* shows the most restricted range, being endemic to SW Africa (from Namibia to Cape Province); *Rhynchocyon* and *Petrodromus* are two forest-dwelling genera occurring respectively in humid and semi-humid tropical forests of central and eastern Africa; *Elephantulus* has a wide disjunct range occurring in southern and south-central Africa (7 species), in the African Horn (2), and only one, *E. rozeti* (Duvernoy, 1833), in Maghreb (NW Africa). Therefore, this clade shows a disjunct Mediterranean and Afrotropical distribution.

In order to evaluate the alternative hypotheses of vicariance or dispersal, firstly it is necessary to clarify the systematic relationships within the order, still today discussed. Several approaches have been attempted using morphological data, by either phenetic (Corbet & Hanks, 1968) or cladistic (Corbet, 1995) analysis, chromosomal (Tolliver et al., 1989), biochemical (Raman and Perrin, 1997), biomolecular (Douady et al., 2003), and geometric morphometric data (Panchetti et al., 2008). All these analyses obtained different conclusions showing a persisting lack of agreement on the phylogeny of the group (for a review on this topic see Panchetti et al., 2008).

The main goal of our study is to give a contribution to the systematic debate on the elephant-shrews, by comparing the results of a geometric morphometric analysis (Panchetti et al., 2008) with the current biogeographical patterns.

MATERIAL AND METHODS

We examined a total of 529 images of dorsal and lateral crania of adult specimens belonging to all the living genera and 13 species of elephant-shrews (Tab. I). Specimens were examined during a visit to three museum collections: the Transvaal Museum (Pretoria, South Africa), the Museum für Naturkunde der Humboldt-Universität zu Berlin (Berlin, Germany), and the Museo Zoologico La Specola, Università di Firenze (Florence, Italy).

Data collected on the genus *Rhynchocyon* were plotted all together since the latter was scarcely represented in the collections examined, and the genus itself was used as outgroup to investigate the relationships within Macroscelidinae. All the following analyses did not consider sexual dimorphism since almost 33% of the entire sample was not sexed. Moreover, juvenile individuals were excluded to minimize the effects of ontogenetic growth, since 8 of 13 species showed only adults. Therefore, we analysed samples only consisting of adult specimens.

A total of 23 (from dorsal side) and 18 (from ventral side) landmarks were fixed in tpsDig (Rohlf, 2001) (Fig. 1) on each cranium image. After digitizing, landmark maps were rotated, scaled (to unit centroid size) and translated through a generalized Procrustes analysis (GPA), i.e. generalized least-squa-

Tab. I - Number of specimens examined for each country and acronym of each species.

Species	Acronym	Country	No. specimens
Macroscelides proboscideus	Mpro	Namibia	11
		South Africa	20
Petrodromus tetradactylus	Ptet	Kenya	3
		Malawi	5
		South Africa	7
		Tanzania	16
		Unknown	3
Rhynchocyon chrysopygus	Rspp	Kenya	1
Rhynchocyon cirnei		Tanzania	8
Rhynchocyon petersi		Tanzania	5
Elephantulus brachyrhynchus	Ebra	Botswana	5
		Malawi	4
		Mozambique	3
		South Africa	16
		Somalia	1
		Zambia	6
		Zimbabwe	8
Elephantulus edwardii	Eedw	South Africa	34
Elephantulus intufi	Eint	Angola	2
		Botswana	8
		Mozambique	1
		Namibia	16
		South Africa	12
Elephantulus myurus	Emyu	Botswana	15
		South Africa	32
		Zimbabwe	1
Elephantulus revoili	Erev	Somalia	9
		Unknown	1
Elephantulus rozeti	Eroz	Algeria	4
		Tunisia	2
		Unknown	4
Elephantulus rufescens	Eruf	Ethiopia	1
		Kenya	1
		Mozambique	1
		Tanzania	10
		Unknown	1
Elephantulus rupestris	Erup	Botwana	1
		Namibia	7
		South Africa	28

res superimposition (GLS) procedure (generalized Procrustes), in order to eliminate scale and orientation distortions, in the process of data collection (Rohlf & Slice, 1990). The coordinates of all aligned specimens were used for the thin-plate splines (Bookstein, 1991; Rohlf, 1993), in order to describe graphically the patterns of shape variation among landmarks and to analyze and display the shape changes among species, the latter visualized with deformation grids depicting differences between objects (Adams et al., 2004). The thin-splate spline procedure was used to fit an interpolated function to an average map (consensus configuration) of the carapace shape and derive the uniform and non-uniform (partial warps) components of shape variation (Bookstein, 1991; Rohlf, 1993). The two uniform components describe differences that affect all parts of the cranium equally (global differences). The non-uniform shape components (partial warps) describe localized departures from the ave-

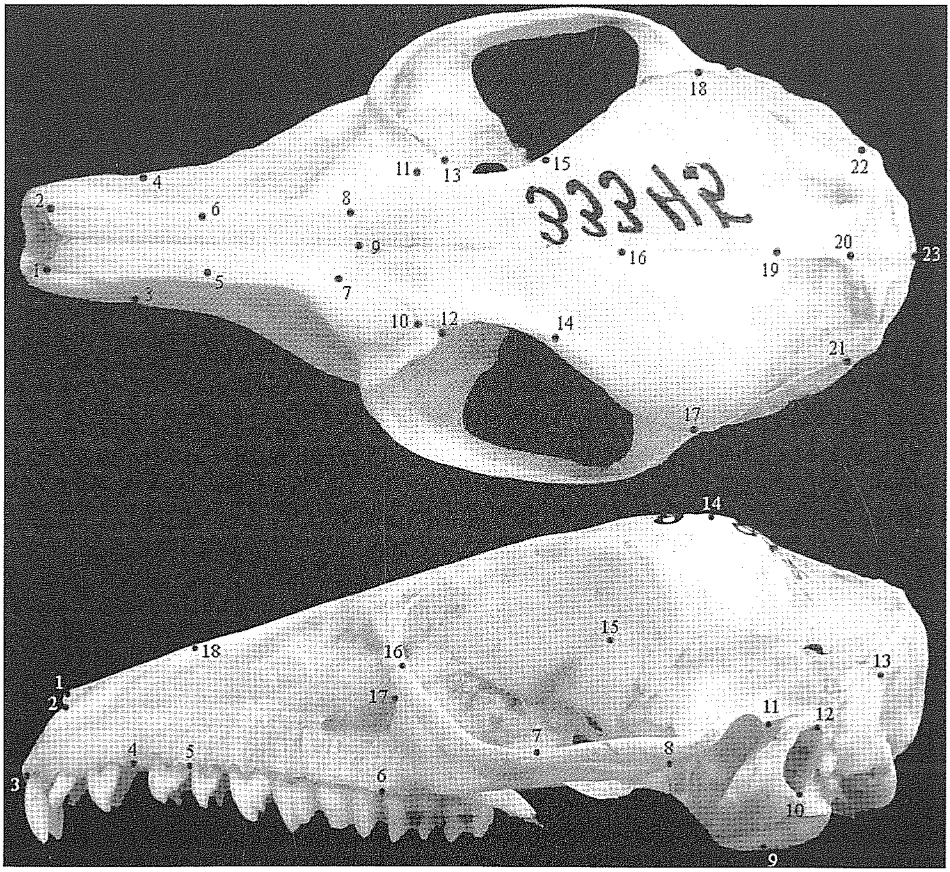


Fig. 1 - Landmarks recorded on the dorsal and lateral side of the cranium of *Petrodromus tetradactylus* (South Africa, Transvaal) (from: Panchetti et al., 2008, *Zoomorphology*).

rage cranium map. Relative warps analysis (RWA, similar to a principal component analysis, using the partial warps scores and the uniform components) was performed to examine the major trends in shape variation (Rohlf et al., 1996; Rohlf, 1998). The ordination method of RWA was performed by the tpsRelw program (Rohlf, 2002). The relative warps (RWs) are the principal components of the variation among specimens in this space (for details see Bookstein, 1991; Rohlf, 1993). In order to assess differences in shape for all age classes and sexes, a multivariate analysis of variance (MANOVA) was performed followed by a series of pairwise Hotelling T^2 tests, using the tpsRegr program (Rohlf, 2000).

Phenetic relationships were investigated through cluster analysis of the Procrustes distances between the mean landmark configurations of each taxa. The unweighted pair-group method using arithmetic average (UPGMA) was chosen in order to detect phenetic relationships among species.

RESULTS

The first two RWs of dorsal and lateral views explained on the whole 64.03% (RW1+RW2=35.20+28.83) and 56.83% (RW1+RW2=38.32+18.51) of the total variance, respectively (Figs. 2 and 3). In both plots three major groups occurred: 1) *Rhynchocyon*; 2) *Macroscelides*; 3) *Petrodromus* + *Elephantulus* species. This result was supported by the MANOVA analysis performed on the RWs (*Wilks'* = 0.0041, $P<0.01$, Generalized Goodall F-test: $F_{10,255} = 12.74$, both for $P<10^{-4}$, *Wilks'* = 0.0041, $P<0.01$, Generalized Goodall F-test: $F_{10,223} = 14.22$, both for $P<10^{-4}$, for dorsal and lateral view, respectively). Hotelling T^2 test proved that not all pairwise comparisons are significant (Tabs. II and III). Non significant differences occurred among species within the *Elephantulus* genus. All other comparisons were significant.

For the dorsal side viewpoint, the distinction between *Rhynchocyon* and all the other Macroscelididae was based on (1) wide nasal bones, (2) wide frontal bones, overhanging orbits and surrounding posterior ends of nasals, (3) narrow supraoccipital bones, (4) anterior ends of nasal bones enlarged, and (5) dividing suture between premaxillar and maxillar bones shifted forwards (i.e. premaxillar shortening and maxillar stretching). Within Macroscelidinae, the first clear-cut separation could be made between *Macroscelides* and the other genera (*Petrodromus* + *Elephantulus*). The extension of bullae in *Macroscelides* pushed forwards supraoccipital, parietal and frontal bones, determining a clear shortening of the nasals and a narrowing of the occipitals. The separation between *Petrodromus* and *Elephantulus* is less easy because of the similar shape of the cranium in these two genera, although the latter showed wider occipitals and slightly narrower frontal bones.

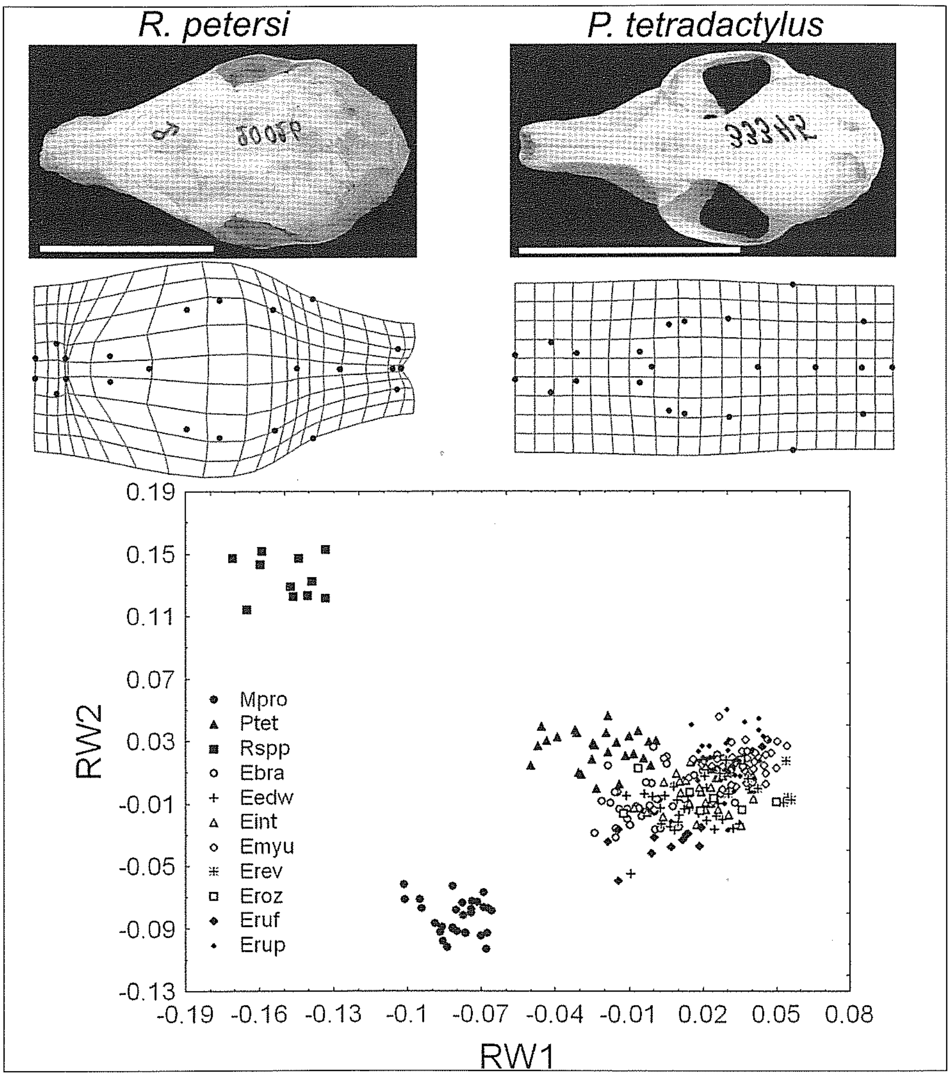


Fig. 2 - Relative Warp Analysis of the cranium dorsal shape and deformation grids for the centroid of each genus. In the sheet we showed images of representative species for plurispecific genera. White bar is equal to 3cm. (from: Panchetti et al., 2008, *Zoomorphology*).

For the dorsal side viewpoint, deformation grids showed that the shape differences between Rhynchocyoninae and Macroscelidinae depended on (1) contraction of the rostral part of the cranium (particularly the premaxillar bones), (2) stretching of the central part of the cranium, due to the elongation of maxillae and frontals (the latter not visible in lateral view), and (3) shearing of the posterior part of the cranium, due to the shifting downwards of temporal and

Tab. II - Distances amongst species. Significant differences obtained by using the Hotelling T^2 test are reported in bold, setting a=0.001, after the Bonferroni correction.

	Ptet	Rspp	Ebra	Eedw	Eint	Emyu	Erev	Eroz	Eruf	Erup
Mpro	7.15	7.15	6.58	7.79	7.66	7.12	4.26	5.70	7.01	7.25
Ptet		7.25	4.57	4.99	5.22	5.12	5.22	5.22	5.25	5.24
Rspp			7.00	6.86	6.23	6.26	6.12	6.22	7.12	7.15
Ebra				1.12	2.22	1.26	2.21	2.04	1.20	2.03
Eedw					1.26	2.15	2.85	1.85	2.15	2.67
Eint						2.25	3.11	1.16	2.33	2.15
Emyu							3.00	1.78	3.05	3.45
Erev								2.15	2.55	2.98
Eroz									1.13	2.27
Eruf										2.33

Tab. III - Distances amongst groups. Significant differences obtained by using the Hotelling T^2 test are reported in bold, setting a=0.001, after the Bonferroni correction.

	Ptet	Rspp	Ebra	Eedw	Eint	Emyu	Erev	Eroz	Eruf	Erup
Mpro	7.87	6.94	7.13	6.25	6.15	7.00	7.05	6.79	6.51	6.33
Ptet		7.49	5.35	6.15	6.01	6.01	6.00	5.75	6.02	5.46
Rspp			7.58	8.01	6.94	7.46	7.13	7.34	6.46	7.30
Ebra				4.99	4.46	4.22	4.27	3.46	4.39	3.25
Eedw					4.06	4.45	4.13	4.33	4.29	4.00
Eint						3.01	4.12	3.90	2.15	3.25
Emyu							3.13	4.01	3.39	3.25
Erev								3.31	3.66	3.55
Eroz									3.59	4.02
Eruf										4.02

supraoccipital bones (grouping landmarks from 9 to 13). In Macroscelidinae, the shape of premaxillar bones was similar for all the species, but slightly contracted in *Macroscelides*. The main differences between the two groups (*Macroscelides* compared to the other two genera) referred to the modified posterior part, mainly due to extreme enlargement of mastoids. The differences between *Petrodromus* and *Elephantulus* were minimal and consisted of the distance between two landmarks (16 and 17).

The phenograms obtained for dorsal and lateral view (Fig. 4) divided Macroscelididae species in two main clusters: the first formed by *Rhynchocyon* and the second including all the other species. In both cases, *Elephantulus* was a "sister" to *Petrodromus*. The two phenograms differed in grouping the *Elephantulus* species, but both showed the group Ebra+Eruf.

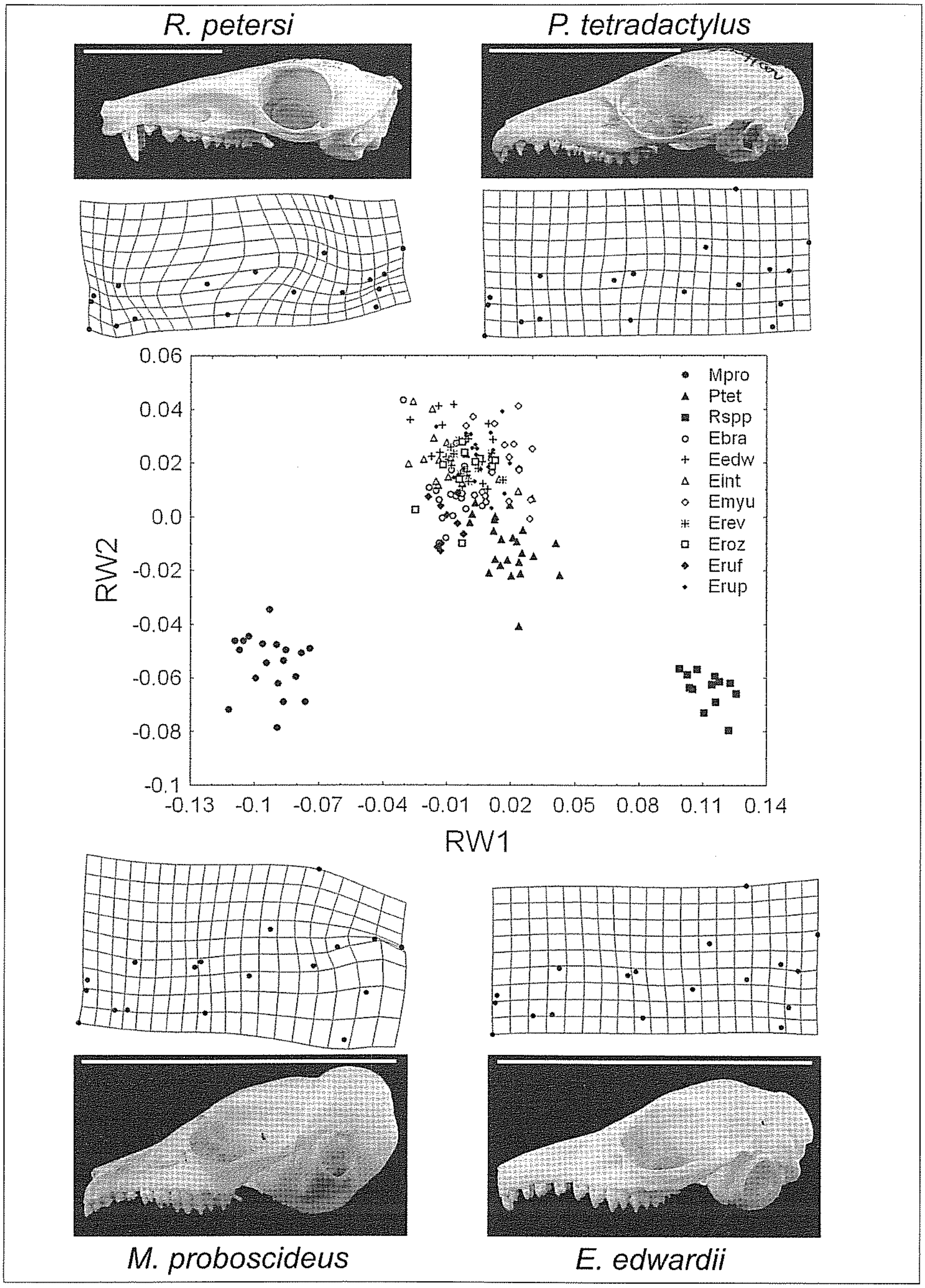


Fig. 3 - Relative Warp Analysis of the cranium lateral shape and deformation grids for the centroid of each genus. In the sheet we showed images of representative species for plurispecific genera. White bar is equal to 3cm. (from: Panchetti et al., 2008, *Zoomorphology*).

DISCUSSION

The geographical distribution of the elephant-shrews has been studied by Corbet and Hansk (1968) in their systematic revision of Macroscelididae. These authors gave a first outline of the known extent range of all the species, then updated by Nicoll & Rathbun (1990), and reconsidered by Boitani et al. (1999) in their Databank for conservation and management of the African mammals. Some of the maps redrawn by the latter report are here attached in order to give examples of distribution for each genus and to define the main chorotypes observed (Figs. 5-9).

The general pattern observed for the whole order is a disjunct distribution at level of the Sahara desert and the absence of these animals from all the western countries of the Afrotropical region. The genus *Elephantulus* occurs in almost all the geographic range occupied by the Macroscelidea (except for the westernmost areas of central Africa). It is also the only genus represented in the Palearctic Region, with one species, *Elephantulus rozeti* (Duvernoy, 1833), which occurs north of Sahara, in Morocco, Algeria and Tunisia; all the other elephant-shrews inhabit the central, eastern and southern parts of the continent.

The absence of elephant-shrews from the Sahara and Sahel zones is probably due to the arid climatic conditions that represent a barrier to dispersal and hamper connectivity between maghrebin and subsaharan representatives of this order. The Afrotropical species of the genus *Elephantulus* occur sparsely, often allopatrically, along the North-South axe extending from the African Horn and the southernmost part of the continent. They are probably the result of allopatric speciation events due to forest growth which produced the isolation of more or less extended blocks of savannah, during the Plio-Pleistocene pluvial/interglacial periods.

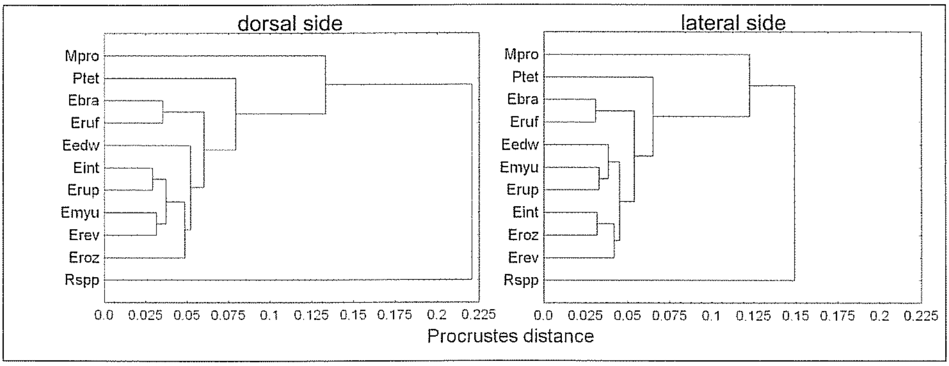


Fig. 4 - Phenetic relationships among species obtained produced by the unweighted pair-group method using arithmetic average analysis for the mean shape of dorsal and lateral sides. (from: Panchetti et al., 2008, *Zoomorphology*).

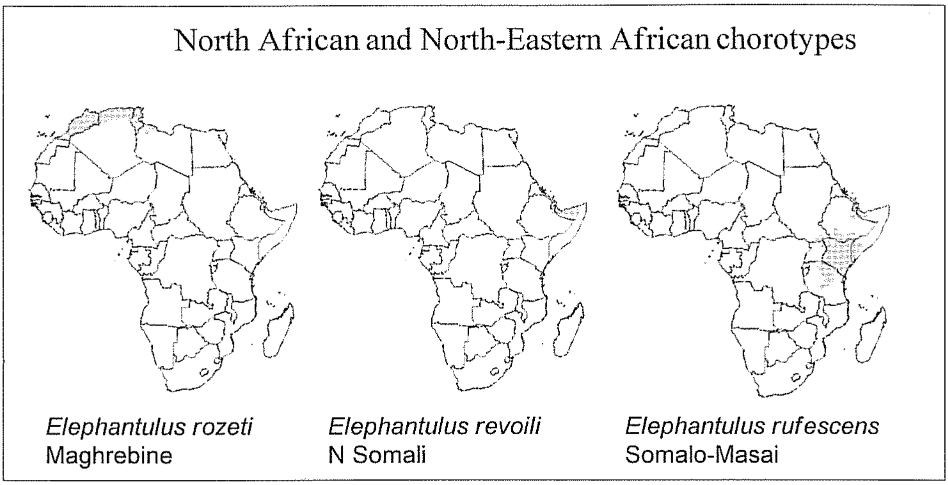


Fig. 5 - Examples of geographic distribution in the genus *Elephantulus*: species with North African and North-Eastern African chorotypes. Only one species, *E. rozeti* (Duvernoy, 1833), occurs north of Sahara; several species, such as *E. revoili* (Huet, 1881) and *E. rufescens* (Peters, 1878), inhabit the savanna/forest mosaic of eastern Africa. (Maps from Boitani et al., 1999).

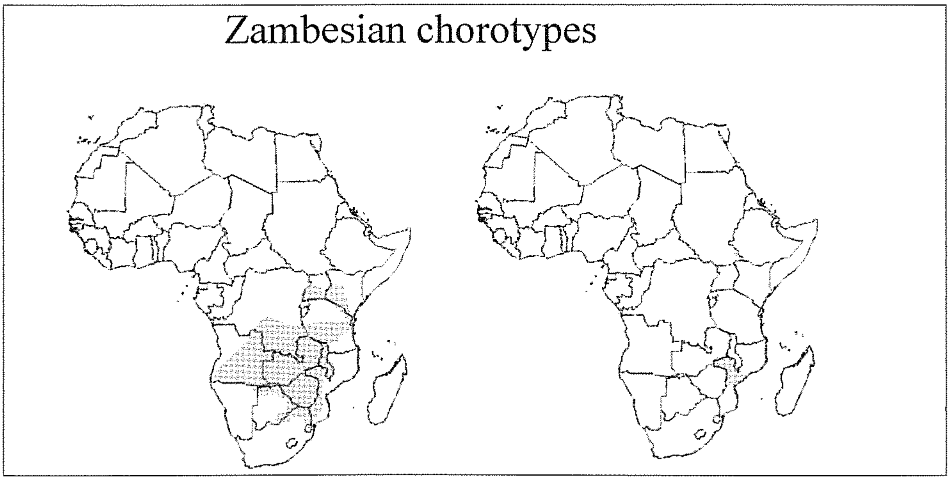
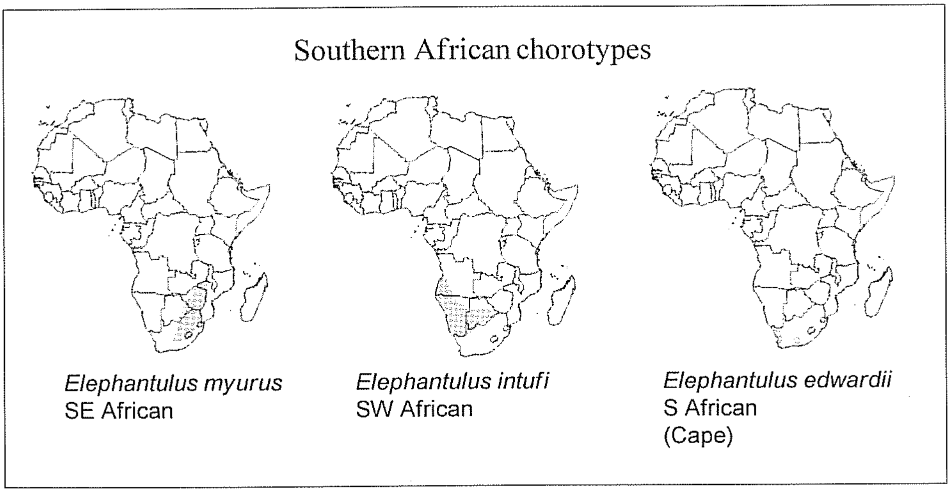


Fig. 6 - Examples of geographic distribution in the genus *Elephantulus*: species with Zambezian chorotypes, whose core area occurs in southeastern Africa. *E. brachyrhynchus* (A. Smith, 1836), *E. fuscus* (Peters, 1852). (Maps from Boitani et al., 1999).

The genus *Rhynchocyon* includes four forest-dwelling species. Its geographic range extends from Central Africa to the coastal forest remnants along the Indian Ocean. Only *R. cirnei* has a wide distribution range; the other species are extremely localized. *Rhynchocyon udzungwensis* Rathbun & Rovero, 2008, was recently discovered and occurs within a restricted area of northern



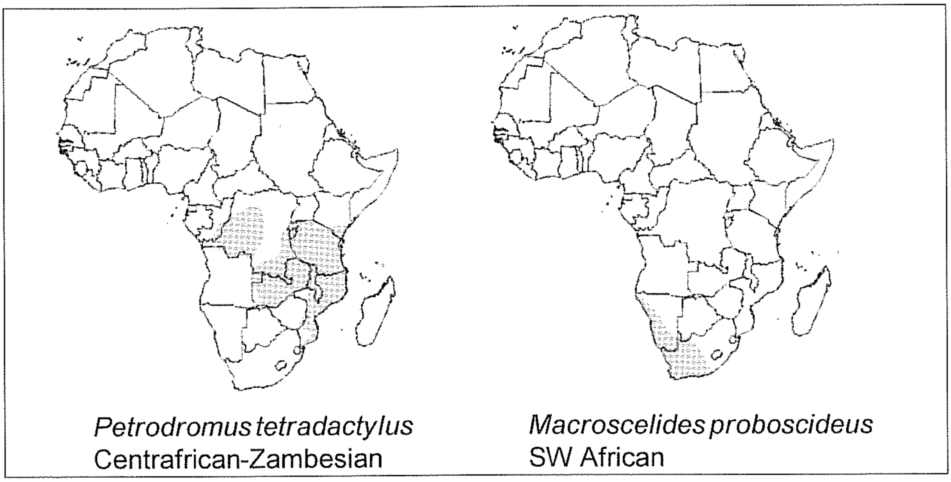
Southern African chorotypes

Elephantulus myurus
SE African

Elephantulus intufi
SW African

Elephantulus edwardii
S African
(Cape)

Fig. 7 - Examples of geographic distribution in the genus *Elephantulus*: species with South African chorotypes. *E. myurus* (Thomas & Schwann, 1906), *E. intufi* (A. Smith, 1836), *E. edwardii* (A. Smith, 1839). (Maps from Boitani et al., 1999).



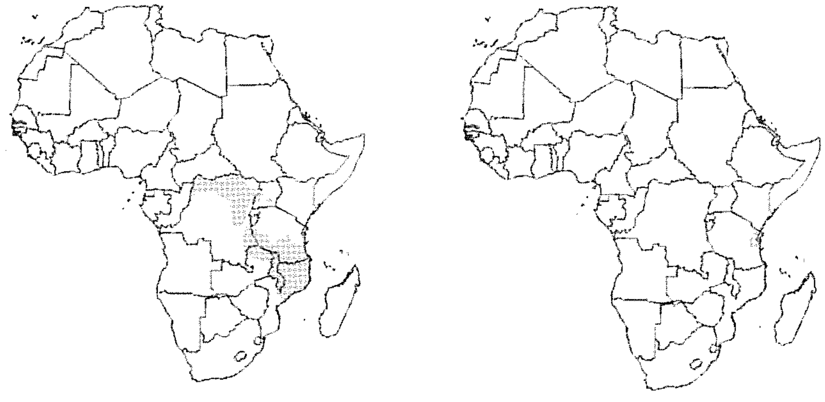
Petrodromus tetradactylus
Centrafrican-Zambesian

Macroscelides proboscideus
SW African

Fig. 8 - Geographic distribution and chorotype of the two monospecific genera: *Petrodromus tetradactylus* (Peters, 1846) and *Macroscelides proboscideus* (Shaw, 1800). (Maps from Boitani et al., 1999).

Udzungwe Mountains (south-central Tanzania) (Rovero et al., 2008). The other two species inhabit a narrow strip of coastal forest in Kenya and Tanzania. They are probably the results of allopatric speciation induced by forest shrinkage during the Plio-Pleistocene interpluvial/glacial periods.

The monospecific genus *Macroscelides*, as many endemic taxa of south-western Africa, represents an adaptation to arid environments and probably



Rhynchocyon cirnei
central-eastern Africa
(N Congo to N Mozambique)

Rhynchocyon petersi
(coast of Tanzania)

Fig. 9 - Examples of geographic distribution in the genus *Rhynchocyon*. Only one species, *R. cirnei* Peters, 1847, has a wide range from central to eastern Africa; the other three species are confined to small ranges. *R. chrysopygus* Günther, 1881, and *R. petersi* Bocage, 1880, occur along a narrow coastal strip in Kenya and Tanzania respectively. *R. udzungwensis* Rathbun & Rovero, 2008, was recently discovered in a restricted area of the Udzungwe mountains, Tanzania. (Maps from Boitani et al., 1999).

resulted by the isolation produced by the miombo forest barrier which separated for long time desert areas of SW from those of NE Africa.

Our study (cf. Panchetti et al., 2008) put in evidence the strong difference between *Rhynchocyon* and all the other species, already evidenced by a classic morphological approach (Corbet & Hanks, 1968), and confirmed the subfamily rank. Cranial features that distinguished Rhynchocyoninae from Macroscelidinae are a consequence of the enlargement of frontal bones, and the reduction of nasal, premaxillar, parietal, and occipital bones. Within Macroscelidinae, the differences between genera were based on modification involving nasals and occipitals. In *Macroscelides*, mastoids became inflated, and this modification made smaller the occipital bones. Moreover, *Macroscelides* showed short nasals respect to the other two genera. *Petrodromus* and *Elephantulus* showed slight differences in the shape of frontals. The shape analysis of the cranium supported the monophyly of *Elephantulus* and its closeness to *Petrodromus*, suggesting that these two genera could represent a single clade. Since the main difference between *Petrodromus* and *Elephantulus* concerns the body size, *Petrodromus* could be considered a giant forest-dwelling representative of *Elephantulus* (cf. Panchetti et al., 2008). The increase of body size seems to be a general trend of forest-dwelling elephant-shrews, also considering the large size of the *Rhynchocyon* species, respect to the smaller size of *Elephantulus* and *Macroscelides* species, which are notoriously a group inhabiting open savannas and dry ecosystems respectively (Rathbun & Fons, 1990; Perrin, 1995).

The clade arrangement resulted from our study agreed with the dendrograms obtained by a biochemical approach conducted by Tolliver et al. (1989), suggesting that *Macroscelides* is the sister group of the remainder Macroscelidinae (*Elephantulus* + *Petrodromus*).

Our phenogram also differed from those obtained by phenetic and cladistic analyses of morphological traits. In fact, Corbet & Hanks (1968) produced a dendrogram on the base of morphological attributes, both skeletal and external, using a purely phenetic approach. Successively, the same data were reassessed in a cladistic analysis (Corbet, 1995) and very similar results were obtained, with *Petrodromus* as the sister-group of the remainder, *Elephantulus* and *Macroscelides*, that represent a single clade. The difference in the results obtained from our analysis and previous morphological approaches, may be explained by the choice of morphological characters used and by the applied methodology. In the classic morphological approach, the traits used to distinguish Macroscelidinae species were mainly external (in example body size, number of mammae, presence/absence of hallux), i.e. characters with little complexity and more easily affected by selective pressure respect to complex structures such as the cranium.

Further approaches to assess phylogeny of elephant-shrews were performed in the last decade. In particular, Raman & Perrin (1997) obtained an unresolved dendrogram where *Macroscelides* and *Petrodromus* resulted closely related while *Elephantulus* appeared a paraphyletic group. Nevertheless, compared with the study of Tolliver et al. (1989), the paper of Raman & Perrin (1997) was based on a narrower set of data and a lower number of both polymorphic loci and specimens. Molecular analyses (Douady et al., 2003) suggested the diphyly of the genus *Elephantulus*, but did not confirm the taxa arrangement proposed by Raman & Perrin (1997). In fact, Douady et al. (2003) separated *E. rozeti* from the other species of the same genus and evidenced its closeness to *Petrodromus* and only secondly to *Macroscelides*.

It seems evident that the subfamily Macroscelidinae represent a problematic group whose right interpretation was not yet achieved. We suppose a common ancestor for the genera *Petrodromus* and *Elephantulus*, that was alike to the living *Elephantulus* species. The evolutionary trend followed by *P. tetradactylus* was probably driven by the colonization of a different ecological niche. This forest colonization did not contribute to develop evident changes of anatomical structures, such as male genitalia and cranium. According to our results, a second evolutionary lineage led to a recent adaptive radiation within the monophyletic genus *Elephantulus*, but such radiation did not involve

E. rozeti. The adaptative radiation of *Elephantulus* drove the savanna-dwelling species to develop a specie-specific mechanism of reproductive isolation based on the shape of penis (Woodall, 1995). We retain that the separation of *P. tetradactylus* and *E. rozeti* from their common ancestor could have occurred before the splitting of the other *Elephantulus* species, conserving some plesiomorphies in the cranium of these two species. According to the opinion of Douady et al. (2003), the colonization of NW Africa by *E. rozeti* is the result of a vicariant event in which the Sahara desertification was instrumental.

ACKNOWLEDGMENTS

We are indebted to Theresa Kearney, curator of mammals at the Transvaal Museum (Pretoria, South Africa), Robert Asher, curator of mammals at the Museum für Naturkunde der Humboldt-Universität zu Berlin (Berlin, Germany), and Paolo Agnelli, curator of Museo Zoologico La Specola, Università di Firenze (Florence, Italy). This study was supported by a grant from the project "Zoogeography of Mediterranean-southern African disjunct distributions by a multimethod approach" (Italian Ministry of Education, University and Research, n. 2004057217), coordinated by Prof. Marco A. Bologna, Roma Tre University, Department of Biology. We received also a financial support of the "European Commission's Research Infrastructure Action via the SYNTHESYS Project". We are also grateful to Luigi Boitani, University of Rome "Sapienza", for the permission to publish the maps from his databank (Boitani et al., 1999).

REFERENCES

ADAMS D.C., SLICE D.E., ROHLF F.J. 2004 - Geometric morphometrics: ten years of progress following the 'revolution'. Ital. J. Zool., 71: 5-16.

BOITANI L., CORSI F., DE BIASE A., D'INZILLO CARRANZA I., RAVAGLI M., REGGIANI G., SINIBALDI I., TRAPANESE P. 1999 - A databank for the Conservation and Management of the African Mammals. European Commission DG VIII/A/1, Bruxelles, and Istituto di Ecologia Applicata, Roma: 1-45, Appendix: 1-1148.

BOOKSTEIN F.L. 1991 - Morphometric tools for landmark data. Cambridge Univerity Press, Cambridge.

CORBET G.B. 1974 Family: Macroscelididae. In: Meester J., Setzer H.W. (eds), The Mammals of Africa: an identification manual, part 1.5. Smithsonian Institution Press, Washington D.C.: 1-6.

CORBET G.B. 1995 - A cladistic look at classification within the subfamily Macroscelidinae based upon morphology. Mammal Rev., 25: 15-18.

CORBET G.B., HANKS J. 1968 - A revision of the elephant-shrews, Family Macroscelididae. Bull. Brit. Mus. Nat. Hist., 16: 47-111.

DOUADY C.J., CATZEFLIS F., RAMAN J., SPRINGER M.S., STANHOPE M.J. 2003 - The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews). Proc. Nat. Acad. Sci., 100: 8325-8330.

KINGDON J. 1974 - East African Mammals. Insectivores and Bats. 2A. University of Chicago Press, Chicago.

NICOLL M.E., RATHBUN G.B. 1990 - African Insectivora and Elephant-shrews. An Action Plan for their Conservation. IUCN, Gland, Switzerland.

PANCHETTI F., SCALICI M., CARPANETO G.M., GIBERTINI G. 2008 - Shape and size variation in the skull of elephant-shrews: a morphometric contribution to a phylogenetic debate. Zoomorphology, 127: 69-82.

PATTERSON B. 1965 - The fossil elephant shrews (Family Macroscelididae). Bull. Mus. Comp. Zool., 133: 295-335.

PERRIN M.R. 1995 - The biology of elephant-shrews. Mammal Rev.,25: 1-100.

RAMAN J., PERRIN M.R. 1997 - Allozyme and isozyme variation in seven southern African elephant-shrew species. Zeitsch. Säugetierk., **62**: 108-116.

RATHBUN G.B. 1979 - The social structure and ecology of elephant shrews. Adv. Ethol., **20**: 1-77.

RATHBUN G.B., FONS R. 1990 - Modern elephant shrews.1. In: Grzimek B. (ed.), Grzimek's encyclopedia of mammals. McGraw-Hill, New York: 520-531.

ROHLF F.J. 1993 - Relative warp analysis and an example of its application to mosquito wings. In: L.F Marcus, Bello E., Garcìa-Valdecasas A. (eds.), Contribution to morphometrics. Museo Nacional de Ciencias Naturales, Madrid: 131-159.

ROHLF F.J. 1998 - On applications of geometric morphometrics to study of ontogeny and phylogeny. Syst. Biol., **47**: 147-158.

ROHLF F.J. 2000 - TpsRegr. Department of Ecology and Evolution, State of New York at Stony Brook, Stony Brook (NY).

ROHLF F.J. 2001 - TpsDig ver. 1.31. Department of Ecology and Evolution, State of New York at Stony Brook, Stony Brook (NY).

ROHLF F.J. 2002 - TpsRelw. Department of Ecology and Evolution, State of New York at Stony Brook, Stony Brook (NY).

ROHLF F.J., SLICE D. 1990 - Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Zool., **39**: 40-59.

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

ROVERO F., RATHBUN G.B., PERKIN A., JONES T., RIBBLE D.O., LEONARD C., MWAKISOMA R.R., DOGGART N. 2008 - A new species of giant sengi or elephant-shrew (genus *Rhynchocyon*) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. J. Zool., London, **274**: 126-133.

SCHLITTER D.A. 1993 - Order Macroscelidea. In: Wilson D.E., Reeder D.M. (eds.), Mammals species of the world. Smithsonian Institution Press, Washington D.C.: 829-830.

SEIFFERT E.R. 2008 - A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. BMC Evol. Biol., 7: 224 doi:10.1186/1471-2148-7-224.

SPRINGER S., CLEVEN G.C., MADESN O., DE JONG W.W., AMRINE H.M., STANHOPE M. 1997 - Endemic African mammals shake the phylogenetic tree. Nature, **388**: 61-64.

STANHOPE M.J., WADDELL V.G., MADSEN O., DE JONG W.W., HEDGES S.B., CLEVEN G.C., KAOI D., SPRINGER M.S. 1998 - Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proc. Nat. Acad. Sci., **95**: 9967-9972.

TOLLIVER D.K., ROBBINS L.W., RAUTENBACH I.L., SCHLITTER D.A., COETZEE C.G. 1989 - Biochemical systematics of elephant shrews from southern Africa. Biochem. Syst. Ecol., **17**: 345-355.

WOODALL P.F. 1995 - The penis of elephant shrews (Mammalia: Macroscelidea). J. Zool., London, **237**: 399-410.