

ORIGINAL INVESTIGATION

Pattern of shape variation in the eastern African gerbils of the genus *Gerbilliscus* (Rodentia, Muridae): Environmental correlations and implication for taxonomy and systematics

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Abstract

Gerbilliscus has been in recent years the subject of new molecular and karyological investigations that shed new light on the evolutionary processes of this taxon. However, the patterns of phenotypic diversification of *Gerbilliscus* remain poorly understood. Furthermore, the molecular phylogenetic analyses posed new questions concerning the systematics and taxonomy of the whole genus and revealed the possible occurrence of cryptic species and hence the need to carry out a taxonomic revision.

We used geometric morphometrics to investigate the adaptive value of morphological changes and to elucidate the systematic relationships and taxonomic status of the *Gerbilliscus* species of east Africa.

Our results show concordance between morphological and genetic species boundaries. However, the observed morphological differences appear not only related to hereditary characters. In fact, the correlation with the climatic variables suggests an adaptive value of shape changes related to different trophic resources availability.

Finally, discriminant analysis of the eastern Africa *Gerbilliscus* species highlight the distinctiveness of *G. vicinus*, clearly separated from *G. robustus* and *G. nigricaudus*.

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Introduction

The genus *Gerbilliscus* Thomas, 1897 is widespread in all sub-Saharan Africa and represents one of the main components of the rodent fauna of arid open habitats. Currently, the genus includes eleven species (Musser and

Carleton 2005) that can be grouped into western, eastern and southern assemblages on the basis of their chromosomal and phylogenetic characteristics (Colangelo et al. 2007). At present, four species are recognized in east Africa: *G. nigricaudus* (Peters, 1879), *G. robustus* (Cretzschmar, 1826), *G. phillipsi* (de Winton, 1898) and *G. leucogaster* (Peters, 1852).

Gerbilliscus has been in recent years the subject of new molecular (Chevret and Dobigny 2005; Colangelo et al. 2005, 2007) and karyological investigations (Qumsiyeh 1986, 1987; Qumsiyeh and Schlitter 1991; Volobouev

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et al. 2007). These analyses have shed new light on the evolutionary patterns of *Gerbilliscus* species and have posed new questions concerning the systematics and taxonomy of the whole genus including both intra- and intergeneric relationships. Particularly, chromosomal (Qumsiyeh 1986; Qumsiyeh et al. 1987, 1991; Volobouev et al. 2007) and mitochondrial DNA (Chevret and Dobigny 2005; Colangelo et al. 2007) analyses have revealed a hidden diversity within the Eastern Africa representatives of this genus and a closer affinity to the Southern African genus *Gerbillurus*. Furthermore, molecular data suggests that the taxonomy and systematics of this genus, traditionally based only on external and cranial morphology (for a revision of east African species see Bates 1985, 1988), present several pitfalls due to the limited discriminating values of some morphological characters previously used to classify the species.

Through cytochrome b and 16S phylogenetic analyses, five taxa have been recognized in East Africa (Colangelo et al. 2005): *G. leucogaster*, *G. robustus*, *G. phillipsi*, *G. nigricaudus*, and *G. vicinus* (Peters, 1878). The last taxon is currently still recognized as a subspecies of *G. robustus* (Musser and Carleton 2005), but molecular analyses strongly suggest that *G. vicinus* should be considered as a distinct species which is closely related to *G. robustus*.

On the basis of its morphological traits, *G. leucogaster* was included by Davis (1966, 1975) in the same species group with the other Eastern African taxa, the “*robustus*” group, while all the remaining species were included in the “*afra*” group. However, the mtDNA analysis (Colangelo et al. 2007) questioned the validity of these two groups suggesting an early divergence of *G. leucogaster* from the other Eastern African taxa and a greater affinity of this species with *G. afra* (Gray, 1830) and *G. brantsii* (Smith, 1836), two endemic species of the Southern African region.

The incongruence between morphological and genetic species boundaries which has become evident in recent years and the possible occurrence of cryptic species within the genus *Gerbilliscus* (Colangelo et al. 2007; Volobouev et al. 2007) suggest that a critical review of the taxonomy and systematics of the genus is required.

The aim of this work was to analyze the morphological skull variation among four East African taxa of the genus *Gerbilliscus* using a geometric morphometric approach (Bookstein 1991; Rohlf and Marcus 1993). To assess the possible adaptive value of the observed morphological changes, we evaluated the correlation between shape and environment comparing shape variation with climatic variables.

Furthermore, we investigated the systematic relationships and taxonomy of eastern African taxa. We evaluated the morphological divergence between *G. leucogaster* and the other three eastern African species for which an early divergence has been suggested

(Colangelo et al. 2007). Then we investigated the taxonomic status of *G. vicinus*, proposed on the basis of molecular analysis (Colangelo et al. 2005). The assessment of correct species boundaries for this genus is important not only for its relevance for taxonomy and systematics but also because *Gerbilliscus* species in East Africa are, together with other murinae genera, one of the principal rodent pests in Eastern Africa (Stenseth et al. 2003).

Material and methods

A total of 108 individuals from East Africa (Sudan, Ethiopia, Kenya and Tanzania) were used. The specimens belong to four different species of the genus *Gerbilliscus*-i.e. *G. leucogaster* (n = 39), *G. nigricaudus* (n = 10), *G. robustus* (n = 11) and *G. vicinus* (n = 48). Specimens come from the collections of the American Museum of Natural History of New York, the National Museum of Natural History of Washington D.C., the Royal Museum for Central Africa of Tervuren and the Museo di Anatomia Comparata “G.B. Grassi” of “Sapienza” University of Rome (for details see Table 1).

From the localities where different species have been found in sympatry (such as *G. vicinus* and *G. nigricaudus* from northern Tanzania, see Fig. 1), we chose only the skulls for which an unambiguous identification (through molecular analysis) was available. From the locality of Dakawa (Tanzania), where *G. vicinus* and *G. leucogaster* were found in sympatry, molecular or chromosomal data were often not available for all the specimens. However, it was possible to use a good sample for both the species due to the presence of a clear distinctive morphological character, i.e. the limits of the posterior palatine foramen which in *G. leucogaster* are located at the level of M₃ reaching the junction of M₁–M₂, while in *G. vicinus*, it extends from the mid-length of M₂ to mid-length of M₁. We tested this character using a large sample of specimens from both the species collected in different localities and unambiguously attributed on the basis of molecular and/or cytogenetic analyses (unpublished data). Finally, samples of *G. robustus* from Sudan were chosen using the museum identification and selecting only paratypes and individuals close to the type locality of the species (Sudan, Ambukol).

The age class of each specimen was established according to the degree of wear of the first lamina of the third mandible molar (classes A–D where A represents the class with the greatest tooth wear), following Bates (1988). Specimens belonging to class D (juveniles) were not included in the analyses.

Images of the dorsal and ventral sides of all the skulls were digitized with a Pixera professional camera. Nineteen landmarks were chosen for the dorsal and twenty-one for the ventral side. Landmarks were collected using the TpsDig software (Rohlf 2004a).

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