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Confrontation of morphological and molecular data: The *Praomys* group (Rodentia, Murinae) as a case of adaptive convergences and morphological stasis

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Abstract

Phylogenetic relationships in a group of 21 African rodent species designated as the *Praomys* group (Murinae) were investigated using morphological characters and sequence data from the complete mitochondrial cytochrome *b* gene and nuclear IRBP gene fragment (840 bp). The molecular results confirm the monophyly of the *Praomys* group, including the species *Malacomys verschureni*, while the other *Malacomys* species appear very divergent. The basal relationships within the *Praomys* group are poorly resolved, suggesting a rapid radiation at about 7–9 million years ago based on genetic divergence rates calibrated from the fossil record. Discrepancies between molecular and morphological results probably reflect of numerous convergences as well as variations in the rates of morphological evolution among lineages. Reconstructions of the ancestral character states suggest a savannah origin for the *Praomys* group, along with some morphological traits conserved by stasis in savannah taxa. At the same time, forest taxa seem to be characterized by an accelerated morphological evolution, with acquisition of convergent adaptive characters.

Keywords: Phylogeny; Morphology; Cytochrome *b*; IRBP; Evolutionary rates; Africa; Adaptation; Stasis

1. Introduction

The so-called *Praomys* group (Rodentia, Murinae) is one of the most diverse and abundant groups of Old World rodents. According to recent findings (Lecompte et al., 2002b, and references therein), a minimum of 40 species belong to this group, following the nomenclature of Musser and Carleton (1993), and including the recent description of *Praomys degraaffi* (Van der Straeten and Kerbis Peterhans, 1999) and *Praomys petteri* (Van der Straeten et al., 2003). The 40 species of the *Praomys* group belong to the following genera: *Colomys* (1 species), *Heimyscus* (1 species), *Hylomyscus* (7 species), *Mastomys* (8 species), *Myomys* (7 species), *Praomys* (11 species), *Stenocephalemys* (2 species), and *Zelotomys* (2 species), and also include a species considered as belonging to the genus *Malacomys* (*Malacomys verschureni*). Ecologically, they have colonized various biotopes in Africa but also part of the Arabian Peninsula (*Myomys yemeni*), ranging from the equatorial rain forest to Sahelian savannas. Their interactions with human populations can have negative consequences with regard to agriculture and human health. The systematics of the group long has been and remains a matter of debate (for review, see Lecompte et al., 2002b). This is partly due to

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the low level of morphological differentiation among the species as well as between the genera, making it difficult to find phylogenetically informative characters (but see Lecompte et al., 2002a, however). The first molecular results obtained in a comprehensive sample of species of this group also point to the possibility of a rapid radiation, that would make it difficult to unravel the phylogenetic relationships within this *Praomys* clade (Lecompte et al., 2002b).

The *Praomys* group phylogeny was recently explored using morphological characters (Lecompte et al., 2002a), but the taxa sampled were not exhaustive for the whole group. At the same time, molecular phylogenetic analyses using the cytochrome *b* (*cytb*) gene sequences (Lecompte et al., 2002b) strongly supported the monophyly of the *Praomys* group (as described here above) and showed the paraphyly of several genera, such as *Praomys*, *Myomys*, and *Stenocephalemys* whose monophyly has been questioned by several earlier studies (e.g., Fadda et al., 2001; Lavrenchenko et al., 1999; Van der Straeten, 1979). However, the resolution provided by *cytb* sequences within the *Praomys* group was weak, possibly due to rapid evolution of the *cytb* gene. Here, we have significantly augmented the sample of species used in the morphological analyses, and we enhanced the genetic analysis by sequencing part of the first exon (ca. 840 bp) of the nuclear gene encoding for the Interphotoreceptor Retinoid Binding Protein (IRBP). This single copy region of nuclear DNA has been used extensively to address questions of mammalian interordinal or interfamilial phylogeny (DeBry and Sagel, 2001; Jansa and Voss, 2000; Jansa and Weksler, 2004; Springer et al., 1997; Stanhope et al., 1996), and also appears useful for discerning relationships at lower taxonomic levels, especially at the generic levels within Murid rodents (Seriwasa et al., 2000; Suzuki et al., 2000; Weksler, 2003).

The nuclear and mitochondrial genes were combined and the phylogenetic trees were compared with those obtained from morphological character analyses within the *Praomys* group. The results provide new insights into the chronological succession of divergence events in this group. Based on divergence time estimates, we discuss some of the possible patterns of differentiation and propose an evolutionary scenario for the group in a clearer spatio-temporal framework. Moreover, the discord between molecules and morphology allows us to link this evolutionary history with trends in the morphological evolution among species in the *Praomys* group.

2. Materials and methods

2.1. Morphological data and species sampling

Morphological characters used in a previous study (Lecompte et al., 2002a) were re-analyzed for an enlarged sample of taxa of the *Praomys* group, including additional *Mastomys*, *Hylomyscus*, and *Myomys* species, as well as the genera *Heimyscus* and *Stenocephalemys*. The genera *Cremnomys*, *Millardia*, *Zelotomys*, and *Colomys* were also integrated into the matrix, according to previous hypotheses based on morphology (Misonne, 1969) and the *cytb* phylogeny results (Lecompte et al., 2002b). From this material (see Lecompte, 2003), the previous morphological matrix produced by Lecompte et al. (2002a) was redefined (see modifications in Supplementary Appendix). The final matrix comprises 35 taxa and 51 characters distributed as: skull (26), dental (15), post-cranial (1), and external or on the soft parts (9). The morphological tree was rooted with *Stochomys longicaudatus*, *Rattus norvegicus*, and *Malacomys longipes*.

The analyses were done both on this final matrix (A) and on two sub-matrices. The first sub-matrix (B) of 30 taxa consists of the *Praomys* group as traditionally defined (hereafter called "*Praomys* group sensu stricto"): *Mastomys*, *Myomys*, *Heimyscus*, *Hylomyscus*, *Praomys*, and *Stenocephalemys*. The genera *Zelotomys* and *Colomys* were added to these 30 taxa to produce the second sub-matrix (C).

The *Mastomys* species are considered a complex of morphologically sibling, chromosomally well differentiated, species (see Granjon et al., 1997; Volobouev et al., 2001, 2002; Denys, in press). Within this genus, all of morphological characters are variable and only a few characters (numbers 11, 22, 45, and 50) allow the differentiation between species. The characters of karyotyped specimens were coded according to the most frequent state observed within the reference sample for each species, in order to try to reconstruct the relationships between these species.

2.2. Species sampling for molecular analyses

The molecular matrix represents 35 species of Murinae comprising 21 from the *Praomys* group (all the genera are represented) and one species from Acomyinae, a subfamily close to the Murinae (cf. Table 1). The species nomenclature used here follows Musser and Carleton (1993).

The *Praomys* group was represented by *P. degraaffi*, *Praomys jacksoni*, *Praomys misonnei*, *Praomys tullbergi*, *M. yemeni*, *Myomys fumatus*, *Myomys albipes*, *Myomys verreauxi*, *Myomys derooi*, *Myomys daltoni*, *Stenocephalemys albocaudata*, *Mastomys coucha*, *Mastomys erythroleucus*, *Mastomys verheyeni*, *Mastomys pernanus*, *Heimyscus fumosus*, *Hylomyscus stella*, *Hylomyscus parvus*. *Zelotomys hildegardeae*, *Colomys goslingi*, and *M. verschureni* were included in the sample following Lecompte et al. (2002b). Two other species of *Malacomys*, i.e., *M. longipes* and *M. edwardsi* were also included here. Also included were the Eurasian murines *Mus musculus*, *R. norvegicus*, *Apodemus* (*Apodemus agrarius* and