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Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy

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ABSTRACT

Within southern Africa, a link between past climatic changes and faunal diversification has been hypothesized for a diversity of taxa. To test the hypothesis that evolutionary divergences may be correlated to vegetation changes (induced by changes in climate), we selected the widely distributed four-striped mouse, *Rhabdomys*, as a model. Two species are currently recognized, the mesic-adapted *R. dilectus* and arid-adapted *R. pumilio*. However, the morphology-based taxonomy and the distribution boundaries of previously described subspecies remain poorly defined. The current study, which spans seven biomes, focuses on the spatial genetic structure of the arid-adapted *R. pumilio* (521 specimens from 31 localities), but also includes limited sampling of the mesic-adapted *R. dilectus* (33 specimens from 10 localities) to act as a reference for interspecific variation within the genus. The mitochondrial COI gene and four nuclear introns (Eef1a1, MGF, SPTBN1, Bfib7) were used for the construction of gene trees. Mitochondrial DNA analyses indicate that *Rhabdomys* consists of four reciprocally monophyletic, geographically structured clades, with three distinct lineages present within the arid-adapted *R. pumilio*. These monophyletic lineages differ by at least 7.9% (±0.3) and these results are partly confirmed by a multilocus network of the combined nuclear intron dataset. Ecological niche modeling in MaxEnt supports a strong correlation between regional biomes and the distribution of distinct evolutionary lineages of *Rhabdomys.* A Bayesian relaxed molecular clock suggests that the geographic clades diverged between 3.09 and 4.30 Ma, supporting the hypothesis that the radiation within the genus coincides with paleoclimatic changes (and the establishment of the biomes) characterizing the Miocene-Pliocene boundary. Marked genetic divergence at the mitochondrial DNA level, coupled with strong nuclear and mtDNA signals of non-monophyly of *R. pumilio*, support the notion that a taxonomic revision of the genus is needed.

1. Introduction

It is well established that global paleoclimatic changes have fundamentally influenced speciation processes through altering the habitats and ranges of species (Hewitt, 2011). Within the southern African context, the onset of xeric conditions towards the end of the Miocene (6.7–6.5 Ma) can be attributed to the glaciation of Antarctica that resulted in rapid cooling of ocean temperatures (Tyson and Partridge, 2000) and the associated intensified upwelling of the Benguela current system (Diester-Haass et al., 2002). In addition, tectonic uplift along the margins of the Great Escarpment approximately 5 Ma (Partridge, 1997; Partridge and Maud, 2000), contributed towards an east-to-west sloping topography and an associated rain-shadow effect across the region. In combination these events resulted in significant vegetation changes across southern Africa and the subsequent establishment of the modern biomes (Coetzee, 1978; Scott et al., 1997). It is thus not surprising that many faunal diversification events within the region date to the Pliocene and Pleistocene (5.3 Ma onwards), and span a diverse range of taxa including reptiles (Bauer and Lamb, 2005; Makokha et al., 2007; Matthee and Flemming, 2002; Portik et al., 2011; Tolley et al., 2006, 2008), small mammals (Russo et al., 2010; Smit et al., 2007; Taylor et al., 2009; Willows-Munro and Matthee, 2009, 2011), and invertebrates (Daniels et al., 2006; Prendini et al., 2003; Price et al., 2007).

The common African four-striped mouse, genus *Rhabdomys* Thomas 1916, was long regarded as monotypic comprising a single species, *R. pumilio* (Sparrman, 1784). The seemingly generalist nature of *Rhabdomys* enables it to maintain a high overall abundance and a wide distribution across a variety of altitudes and habitat

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types (de Graaff, 1981; Skinner and Chimimba, 2005). In southern Africa the taxon occurs throughout most of Namibia, Botswana, Zimbabwe, Mozambique, Swaziland, Lesotho, and South Africa (Fig. 1), but is also found in Tanzania, Kenya, Uganda, the DRC, Angola, Zambia, and Malawi (Castiglia et al., 2012; Rambau et al., 2003; Skinner and Chimimba, 2005). Extensive variation in pelage color and morphology resulted in the description of 20 subspecies from southern Africa alone (Roberts, 1951), but Meester et al. (1986) regarded seven as being valid (Fig. 1).

The exact distributional limits of the proposed subspecies are poorly understood (Skinner and Chimimba, 2005). Allozyme analysis (Mahida et al., 1999) has failed to clearly describe the variation within the genus, and breeding studies (Pillay, 2000a,b) have been inconclusive in ascertaining whether more than one species is present (Musser and Carleton, 2005). Based on variable chromosome numbers and the presence of two distinct mtDNA clades within *Rhabdomys*, two geographically distinct species, *R. pumilio* and *R. dilectus*, are currently recognized (Musser and Carleton, 2005; Rambau et al., 2003). Within the subregion, the mesic-adapted *R. dilectus* ($2n = 46$ and $2n = 48$) has an eastern distribution in South Africa, Zimbabwe, Uganda, and Tanzania, and the xeric-adapted *R. pumilio* ($2n = 48$) occurs widely in the arid central and western regions of South Africa, Namibia, and Botswana. Rambau et al. (2003) further distinguished two subgroups with different cytotypes within *R. dilectus*, representing what they refer to as the subspecies *R. d. dilectus* ($2n = 46$) and *R. d. chakae* ($2n = 48$). A recent study has shown that *R. dilectus* is even more diverse and consists of at least three distinct mitochondrial lineages (Castiglia et al., 2012).

Specific factors driving the diversification within *Rhabdomys* are not well defined. It has been suggested that the arid-adapted *R. pumilio*, with a western distribution, forms social groups in the Succulent Karoo Biome as a result of habitat saturation (Schradin et al., 2010; Schradin and Pillay, 2004) whereas *R. dilectus* in the east is solitary within the mesic grassland due to the lower abundance and higher dispersion of food resources (Schradin and Pillay, 2005). Since large scale changes in the distributions of vegetation have been directly linked to diversification among lineages (Edwards et al., 2011; Linder et al., 2010; Tolley et al., 2008), a prediction can be made that different biomes could harbor distinct evolutionary lineages of the four-striped mouse. Importantly, should this pattern emerge in *Rhabdomys*, it will not be unique. Biomes have previously been found to harbor distinct taxon groups (Chimimba, 2001; Russo et al., 2010) and there is now extensive evidence of secondary contact among distinct faunal lineages where vegetation types/biomes meet (Engelbrecht et al., 2011; Tolley et al., 2004, 2010; Willows-Munro and Matthee, 2011). Particularly relevant to *Rhabdomys* would be the "Bedfort-gap" (Fig. 2; Lawes, 1990), which represents a complex region where several biomes meet (Mucina and Rutherford, 2006). The region is interspersed within the transitional Albany Thicket Biome (Vlok and Euston-Brown, 2002), contains elements of a variety of vegetation types (Mucina and Rutherford, 2006) and also provides the interface between the all-year rainfall zone and the summer-rainfall zone (Chase and Meadows, 2007).

To test the hypothesis that changes in vegetation resulted in evolutionary divergences in the four-striped mouse, *Rhabdomys*, we investigated the spatial genetic structure of *R. pumilio*, which has a distribution spanning six biomes (*sensu* Mucina and Rutherford, 2006; Fynbos, Nama-Karoo, Succulent Karoo, Desert, Savanna, and Albany Thicket) across the mainly arid regions of South Africa and Namibia. *Rhabdomys dilectus* from the mesic regions of the Grassland and Savanna Biomes were included as a reference taxon to provide estimates of interspecific variation within the genus. A Bayesian relaxed molecular clock was used to date divergences among geographic assemblages and ecological niche modeling was applied to better understand the influence of present and past climatic conditions on the potential distribution of *R. pumilio*.

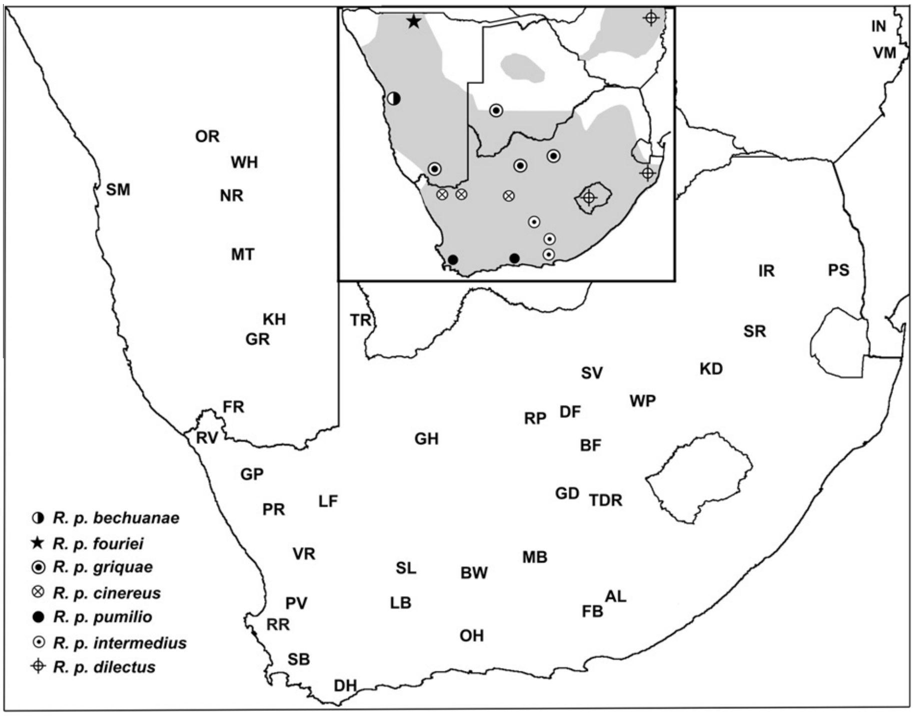

Fig. 1. Localities from which specimens were analyzed in this study with codes as in Table 1. The localities from which subspecies (following Meester et al., 1986) have been described and the shaded distribution of *Rhabdomys* within southern Africa are indicated in the insert.