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Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles

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Abstract

Using sequences of the mitochondrial 16S rRNA gene, we reconstructed the phylogeography of six widely distributed Malagasy reptiles: two gekkonid lizard species, *Phelsuma lineata* and *Hemidactylus mercatorius*; two chameleons, the *Calumma brevicorne* complex, and *Furcifer lateralis*; and two skinks, *Trachylepis gravenhorstii* and *Trachylepis elegans*. Genetic differentiation among major haplotype lineages was high and in some cases indicates or confirms species status of the divergent populations. Maximum uncorrected sequence divergences were between 2.2% and 8.3% within the various species or species complexes. Haplotype lineages were exclusive to geographic regions, except in the commensal *H. mercatorius* where in three anthropogenic habitats coexistence of haplotype lineages was observed, possibly due to human translocation. The eastward flowing rivers Mangoro and Mananara may represent barriers to gene flow in the case of three species each. Some species sampled from humid eastern and arid western Madagascar showed no differentiation between populations from these two regions; instead the pattern observed was in several cases more concordant with a differentiation along a north-south axis.

Keywords: Madagascar; Phylogeography; Squamata; *Calumma brevicorne*; *Calumma amber*; *Calumma crypticum*; *Furcifer lateralis*; *Phelsuma lineata*; *Hemidactylus mercatorius*; *Trachylepis gravenhorstii*; *Trachylepis elegans*

1. Introduction

The island of Madagascar is known for its particular geographic history and for the high level of endemism of its biota (e.g., Goodman and Benstead, 2003). Its biodiversity is not only extraordinarily distinctive and diverse, but also endangered, making its exploration an urgent matter. The knowledge of even its vertebrates is far from complete, and new species have been discovered and described at a vigorous pace in the last few years (Yoder et al., 2005).

Madagascar's bioclimatic zonation follows a primary east-west division. A central chain of mountains spaced in north-south direction causes the humidity transported by eastern trade winds to rain down on the eastern escarpment where humid tropical rainforest occurs. Little rainfall reaches the west and especially the south, where dry deciduous forests and arid spiny forest (in the south-west) is the predominant type of vegetation.

Based on the opening of the Indian Ocean by the northward drift of India, and the correlated onset of the trade winds that reach Madagascar, Wells (2003) estimates the origin of the Malagasy eastern rainforests in the Eocene or Oligocene. In the northern fourth of Madagascar, the rainforests occupy much of the center and reach the north-western coast around the Sambirano estuary. Here they are formed by a special kind of monsoon rainforest of possibly younger Late Miocene or Pliocene age (Wells,

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2003). Schatz (1999) also divides Madagascar into a bioclimatic eastern and a western region, each of which are subdivided into several domains. Much of the northern fourth of Madagascar is included in the eastern region. A zoogeographical zonation proposed to explain the distribution of Madagascar's reptiles (Angel, 1942) is largely in agreement with this bioclimatic zonation (Glaw and Vences, 1994: 11–14), cf. Fig. 1. Several studies have supported east-west vicariance causing species formation in Madagascan vertebrates. Thus, in the context of recurrent climatic oscillations, this may well have been one of the triggers causing the large species diversity in Madagascar's fauna. The underlying process would be that the sharp ecological distinction between eastern and western habitats constitutes a barrier to gene flow, causing a basal split between eastern and western clades in the phylogeography of species of initially wide distribution, eventually leading to speciation. Yoder and Heckman (2006) refer to this hypothesis as the 'ecogeographic constraint'.

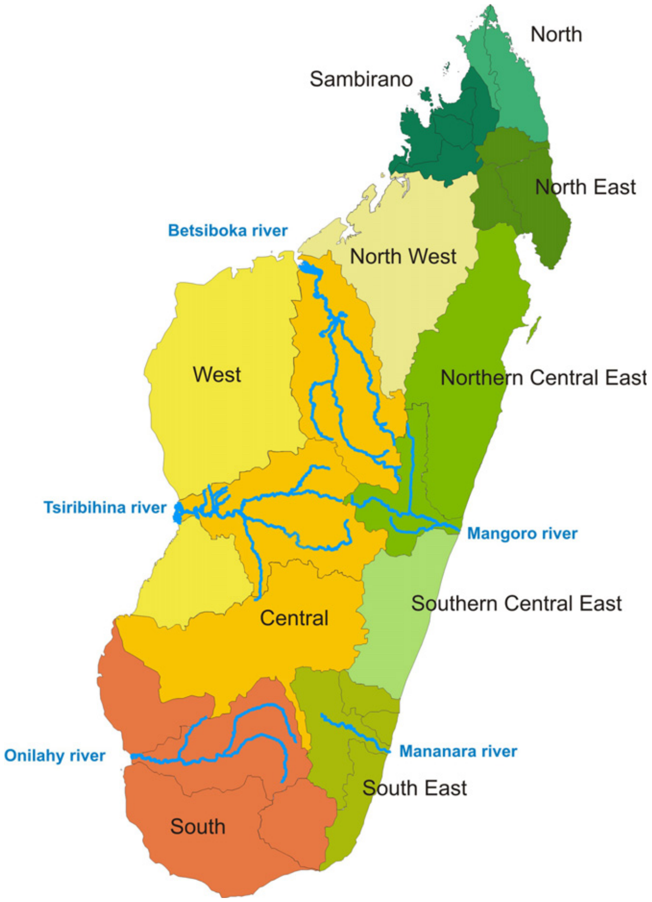

Fig. 1. Biogeographic regions of Madagascar as used in this paper. Lines delimit centers of endemism and refuges from the hypothesis laid out by Wilmé et al. (2006). Major rivers are depicted in blue. Different colors denote groups of these endemism centers and refuges that roughly fit the biogeographic regions as defined by Angel (1942) and Glaw and Vences (1994) for amphibians and reptiles. Pending future analyses, these regions as used here are not be understood as an explicit hypothesis of a biogeographically meaningful zonation, but merely as definition to facilitate referring to particular areas of Madagascar in the text. Five major rivers (Mangoro, Mananara, Betsiboka, Tsiribihina and Onilahy) that may be relevant as barriers for gene flow in the species discussed herein are highlighted. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

In reptiles, the examples of east-west vicariance come from species pairs such as the geckos *Ebenavia inunguis* (east) and *Ebenavia maintimainty* (west), *Matoatoa spannringi* (east) and *Matoatoa brevipes* (west), and *Paragehyra gabriellae* (south-east) and *P. petiti* (west), and the boid snake subspecies *Sanzinia madagascariensis madagascariensis* (east) and *S. m. volontany* (west) (Nussbaum and Raxworthy, 1998; Nussbaum et al., 1998; Vences and Glaw, 2003). Similar examples from the amphibians include the treefrogs *Boophis albilabris* (east) and *Boophis occidentalis* (west), and *Boophis tephraeomystax* (east) and *Boophis doulioti* (west) (Andreone et al., 2002; Glaw and Vences, 1994: 90; Vences and Glaw, 2002).

However, (Yoder and Heckman (2006)) have recently challenged this traditional perspective on Madagascar's biogeography. They show that in mouse lemurs of the genus *Microcebus* the primary phylogenetic split, instead of being between east and west, is between a northern and a southern clade. Each clade contains several species, spread over the diverse ecological habitats of east and west, without recurrent east-west vicariant patterns at shallower phylogeographic levels (Yoder and Heckman, 2006; Yoder et al., 2000). Deep interspecific north-south splits can also be found in the dwarf chameleons of the genus *Brookesia* (Raxworthy et al., 2002) and in the colubrid snake genus *Madagascarophis* (Nagy et al., in press); a vicariant north-south pattern of sister species pairs occurs in several reptile groups, e.g., the boids *Acrantophis madagascariensis* (north) and *Acrantophis dumerili* (south), the geckos *Uroplatus alluaudi* (north) and *Uroplatus malahelo* (south), and the chameleons *Brookesia lolontany* (north) and *Brookesia nasus* (south) (Nussbaum and Raxworthy, 1994; Raxworthy and Nussbaum, 1995; Vences and Glaw, 2003). Interestingly, there is no obvious biogeographic barrier which would explain this primary biogeographic division between north and south.

Early studies on lemur biogeography (Martin, 1972) have proposed a division of Madagascar that is largely congruent with the one of Angel (1942), reflecting the same climatic conditions that differentiate the central highlands, the east coast, and the West and South. Multi-species phylogeographic studies (Pastorini et al., 2003) have emphasized the importance of three large rivers as barriers in species distribution. Wilmé et al. (2006) postulate that river basins at intermediate altitude functioned as stable refugia during cold glacial periods. Climatic oscillations have caused forests to move up and down the slopes, enabling and severing gene flow and thereby promoting speciation (cf. Fig. 1).

Although the complex topography of northern Madagascar may be seen as predictive of intensive speciation (Raxworthy and Nussbaum, 1995), none of these models provides a convincing explanation for the origin and main-