



Molecular phylogeny of Neotropical rock frogs reveals a long history of vicariant diversification in the Atlantic forest

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ABSTRACT

The Brazilian Atlantic coastal forest is one of the most heterogeneous morphoclimatic domains on earth and is thus an excellent region in which to examine the role that habitat heterogeneity plays in shaping diversification of lineages and species. Here we present a molecular phylogeny of the rock frogs of the genus *Thoropa* Cope, 1865, native to the Atlantic forest and extending to adjacent *campo rupestre* of Brazil. The goal of this study is to reconstruct the evolutionary history of the genus using multilocus molecular phylogenetic analyses. Our topology reveals 12 highly supported lineages among the four nominal species included in the study. Species *T. saxatilis* and *T. megatympenum* are monophyletic. *Thoropa taophora* is also monophyletic, but nested within *T. miliaris*. Populations of *T. miliaris* cluster in five geographically distinct lineages, with low support for relationships among them. Although all 12 lineages are geographically structured, some *T. miliaris* lineages have syntopic distributions with others, likely reflecting a secondary contact zone between divergent lineages. We discuss a biogeographic scenario that best explains the order of divergence and the distribution of species in Atlantic forest and adjacent areas, and outline the implications of our findings for the taxonomy of *Thoropa*.

1. Introduction

The Brazilian Atlantic forest is a highly complex and heterogeneous morphoclimatic and phytogeographic domain (Ab'Saber, 1977). It is a global biodiversity hotspot (Mittermier et al., 1998; Morellato and Haddad, 2000; Silva and Casteleti, 2003) and high habitat heterogeneity, resulting from topographic complexity and large latitudinal range, is one of the main reasons proposed for its high biological diversity (Ribeiro et al., 2009; Rodríguez et al., 2015). Therefore, the Atlantic forest is an excellent region to examine how heterogeneous habitats contribute to diversification (Rodríguez et al., 2015). Habitat heterogeneity has a potentially large effect on amphibian diversification, due to their low vagility and often specialized habitat preferences (Rodríguez et al., 2015). Indeed, the Atlantic forest is home to more than 500 frog species (Haddad et al., 2013; Toledo et al., 2014), accounting for 8.1% of the world's known anuran diversity. More than

75% of Atlantic forest anurans are endemic to the domain (Haddad et al., 2013) and many of these endemic species inhabit montane environments (Cruz and Feio, 2007; Haddad et al., 2013).

Rock frogs in the genus *Thoropa* Cope, 1865, belong to the family Cycloramphidae (*sensu* Frost, 2017) and include the following six species endemic to Brazil: *T. miliaris* (Spix, 1824), *T. petropolitana* (Wandolleck, 1907), *T. taophora* (Miranda-Ribeiro, 1923), *T. lutzi* Cochran, 1938, *T. megatympenum* Caramaschi and Sazima, 1984, and *T. saxatilis* Cocroft and Heyer, 1988. All species of the genus, except *T. megatympenum*, inhabit rocky seashores, wet rocky outcrops, and boulders and waterfalls in montane rocky streams of the Atlantic forest (Bokermann, 1965; Cocroft and Heyer, 1988; Feio et al., 2006). *Thoropa megatympenum* inhabits the Atlantic forest-Cerrado and Atlantic forest-Caatinga ecotones (Caramaschi and Sazima, 1984) in the same kinds of habitats as its congeners. *Thoropa* species have specialized breeding requirements. Males are typically territorial and exhibit parental care of

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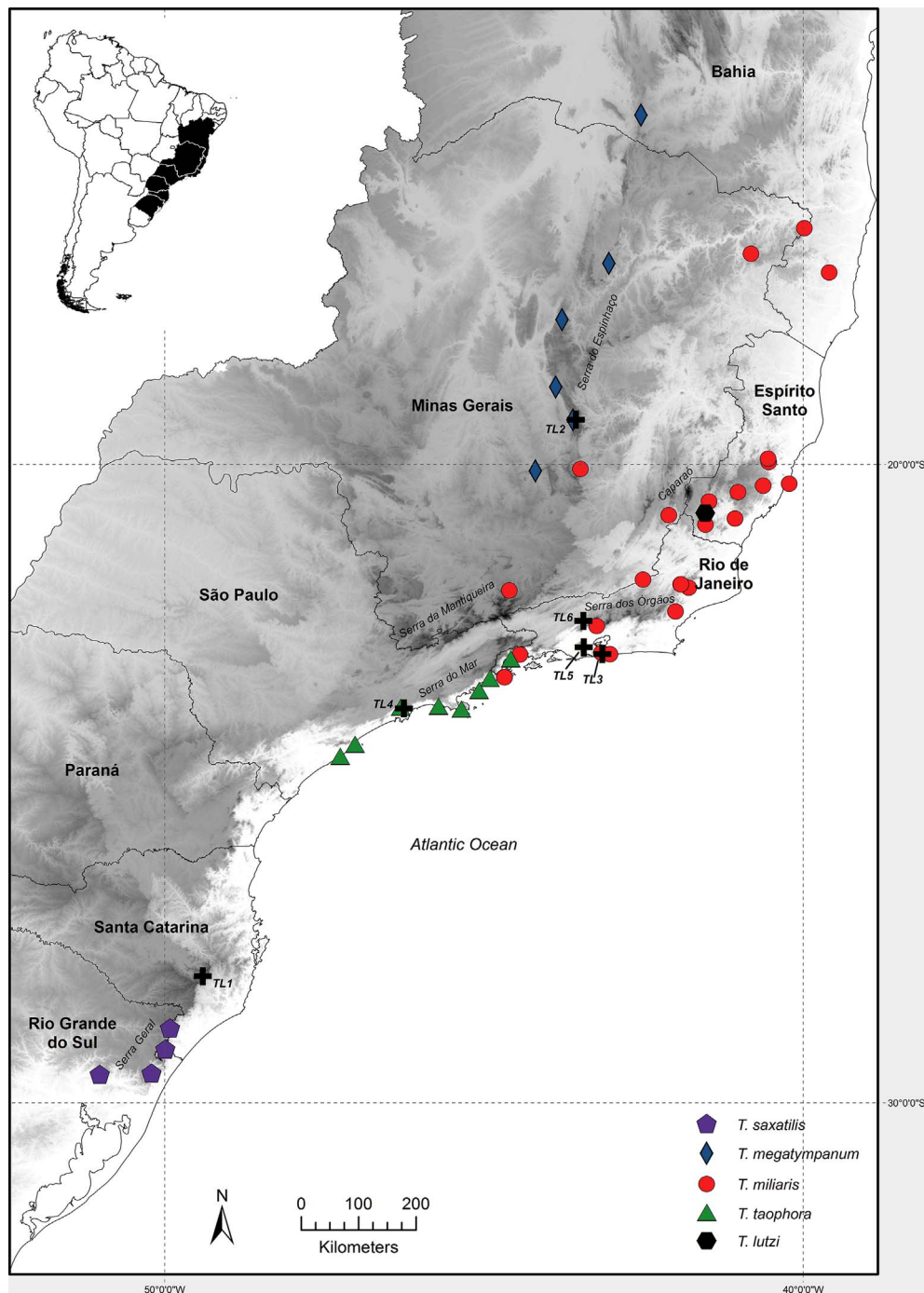


Fig. 1. Collection localities for *Thoropa* samples included in this study. Black crosses labelled TL1–TL6 indicate type localities of *T. saxatilis*, *T. megatympnum*, *T. miliaris*, *T. taophora*, *T. lutzi* and *T. petropolitana*, respectively. Elevation is shown in gray scale ranging from white (0–50 m above the sea level) to black (3900–3950 m above sea level).

egg clutches (Giaretta and Facure, 2004; Muralidhar et al., 2014; Consolmagnò et al., 2016), which are deposited on rocks in freshwater seeps or at the humid rocky margins of shallow rivulets (Barth, 1956; Bokermann, 1965; Rocha et al., 2002). Tadpoles are exotrophic and semiterrestrial, hatching and developing in the water seeps (Barth, 1956; Bokermann, 1965).

A phylogeographic study of *Thoropa miliaris* and *T. taophora* showed that populations of the southern *T. taophora* are monophyletic, and nested within the northern *T. miliaris*, and inferred a north to south expansion and differentiation within these two species (Fitzpatrick et al., 2009). The relationships of these two species to the others in the genus and the mechanisms potentially contributing to their

diversification are still unknown. In this study we reconstruct a multi-locus phylogeny for populations of all available species within the genus *Thoropa*.

Our specific goals are to (1) describe the spatial distribution and genetic diversity of species and cryptic lineages within the genus; (2) infer the phylogenetic relationships of *Thoropa* species using mitochondrial and nuclear markers and date divergences among species and lineages; and (3) test for monophyly of the genus *Thoropa* and each of the nominal species within the genus. We discuss our results in the context of a biogeographic scenario that best explains the order of divergence and the current distribution of species in Atlantic forest and adjacent areas.

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