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Biogeographic links between southern Atlantic Forest and western South America: Rediscovery, re-description, and phylogenetic relationships of two rare montane anole lizards from Brazil

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ABSTRACT

Data on species ranges and phylogenetic relationships are key in historical biogeographical inference. In South America, our understanding of the evolutionary processes that underlie biodiversity patterns varies greatly across regions. Little is known, for instance, about the drivers of high endemism in the southern montane region of the Atlantic Rainforest. In this region, former biogeographic connections with other South American ecosystems have been invoked to explain the phylogenetic affinities of a number of endemic taxa. This may also be the case of the montane anole lizards *Anolis nasofrontalis* and *A. pseudotigrinus*, known from few specimens collected more than 40 years ago. We combine new genetic data with published sequences of species in the *Dactyloa* clade of *Anolis* to investigate the phylogenetic relationships of *A. nasofrontalis* and *A. pseudotigrinus*, as well as estimate divergence times from their closest relatives. Based on newly sampled and previously overlooked specimens, we provide a taxonomic re-description of those two taxa. Our phylogenetic analysis recovered six main clades within *Dactyloa*, five of which were previously referred to as species series (*aequatorialis*, *heterodermus*, *latifrons*, *punctatus*, *roquet*). A sixth clade clustered *A. nasofrontalis* and *A. pseudotigrinus* with *A. dissimilis* from western Amazonia, *A. calimae* from the Andes, *A. neblininus* from the Guiana Shield, and two undescribed Andean taxa. We therefore define a sixth species series within *Dactyloa*: the *neblininus* series. Close phylogenetic relationships between highly disjunct, narrowly-distributed anoles suggest that patches of suitable habitat connected the southern Atlantic Forest to western South America during the Miocene, in agreement with the age of former connections between the central Andes and the Brazilian Shield as a result of Andean orogeny. The data also support the view of recurrent evolution (or loss) of a twig anole-like phenotype in mainland anoles, in apparent association with the occurrence in montane settings. Our findings stress the value of complementary genetic sampling efforts across South American countries to advance studies of mainland anole taxonomy and evolution.

1. Introduction

Despite more than 250 years of biodiversity inventories, the rate of biological discoveries in the Neotropics remains high (Pimm et al., 2010; Scheffers et al., 2012), continuously transforming our understanding of regional biogeographic patterns and their underlying ecological and evolutionary processes (Angulo and Icochea, 2010). Biological discoveries often come from well-studied areas, as is the case of the Atlantic Rainforest, a biodiversity hotspot in eastern Brazil. In this region, recent expeditions have led to the description of several squamate and amphibian species (e.g., Rodrigues et al., 2007, 2009, 2013; Teixeira Jr. et al., 2012, 2013), and in some cases to the rediscovery of species that have remained undetected for decades (e.g., Pirani et al., 2010; Tonini et al., 2011; Zaher et al., 2005). Refining our knowledge about species ranges and phylogenetic relationships is key to improving inferences of

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historical biogeography and the drivers of diversification in the highly diverse and increasingly threatened Neotropical region (Angulo and Icochea, 2010).

In South America, our understanding of the historical processes that have shaped biodiversity patterns varies greatly across regions. Several investigations have found evidence of former connections and biotic exchange between the northern Atlantic Forest and eastern Amazonia, which resulted in high taxonomic similarity among them (e.g., Batalha-Filho et al., 2013; Fouquet et al., 2012a, b; Prates et al., 2016a,b). By contrast, little is known about the historical processes that have shaped high levels of biodiversity in the cooler mountains that characterize the southern Atlantic Forest (Amaro et al., 2012). In this region, contemporary climate heterogeneity strongly correlates with lineage endemism (Carnaval et al., 2014), while phylogenetic patterns within bird, frog and rodent clades suggest historical connections and biotic exchange with the Andean Yungas and western Amazonia (e.g., Batalha-Filho et al., 2013; Castroviejo-Fisher et al., 2014, 2015; Percequillo et al., 2011). The disjunct distribution of some squamates further points to biogeographic links between the southern Atlantic Forest and western South American ecosystems, as in the well-known case of the of anguid lizard *Diploglossus fasciatus* (Gray, 1831) (Vanzolini and Williams, 1970).

Ancient forest connections may explain the phylogenetic and taxonomic affinities of two rare endemic southern Atlantic Forest anole lizards, *Anolis nasofrontalis* Amaral, 1933 and *Anolis pseudotigrinus* Amaral, 1933 (Fig. 1). So far, both species are represented by only a few specimens collected more than 40 years ago in two adjacent sites in the Brazilian state of Espírito Santo. These two sympatric species are characterized by small to medium size, short limbs, lichenous coloration, and large smooth head scales. These traits have been interpreted as reminiscent, at least in part, of the Greater Antillean "twig anole" ecomorph, and therefore may provide evidence of adaptive convergence between mainland and Caribbean anoles (Poe et al., 2015; Losos et al., 2012; Williams, 1976, 1992). Morphologically, *A. nasofrontalis* and *A. pseudotigrinus* contrast from the other three native Atlantic Forest anoles, *Anolis fuscoauratus* D'Orbigny in Duméril and Bibron, 1837, *Anolis ortonii* Cope, 1868, and *Anolis punctatus* Daudin, 1802, which occur predominantly in the northern Atlantic Forest lowlands (although expanding into a limited extent of southern Atlantic Forest). On the other hand, a twig anole-like phenotype is also present in a number of South American species from the Andes and Guiana Shield (e.g., Losos et al., 2012; Poe et al., 2015; Williams, 1976; Williams et al., 1996), which may be indicative of close phylogenetic relationships with *A. nasofrontalis* and *A. pseudotigrinus*. However, because of the small number of collected specimens and lack of genetic samples, we know very little about the evolution and biogeographic relationships of these two rare Atlantic Forest endemics.

Through targeted herpetological inventories in the Atlantic Forest, we recently obtained new samples of *Anolis nasofrontalis* and *A. pseudotigrinus*. We also identified specimens that have been deposited in zoological collections yet previously overlooked or misidentified. By combining new genetic data with published sequences of other species in the *Dactyloa* clade of *Anolis* (Castañeda and de Queiroz, 2011; Poe et al., 2015; Prates et al., 2015), we investigate the phylogenetic relationships of *A. nasofrontalis* and *A. pseudotigrinus* and estimate divergence times from their closest relatives. Based on the morphological attributes of newly collected, previously collected, and type specimens, we provide a much-needed taxonomic re-description of *A. nasofrontalis* and *A. pseudotigrinus*.

Our analysis incorporates molecular data generated by previous phylogenetic assessments of *Dactyloa*, yet we do not reexamine the group's systematics beyond our target taxa and their closest relatives. Instead, we refer to the much more extensive work of Castañeda and de Queiroz (2013) and Poe et al. (2015).

2. Material and methods

2.1. Sampling of molecular data

Newly sampled *Anolis nasofrontalis* and *A. pseudotigrinus* were collected in the Reserva Biológica Augusto Ruschi, state of Espírito Santo, coastal southeastern Brazil (−19.917, −40.552, WGS1984). For molecular phylogenetic inference, we matched available genetic datasets (see below) and sequenced the mitochondrial

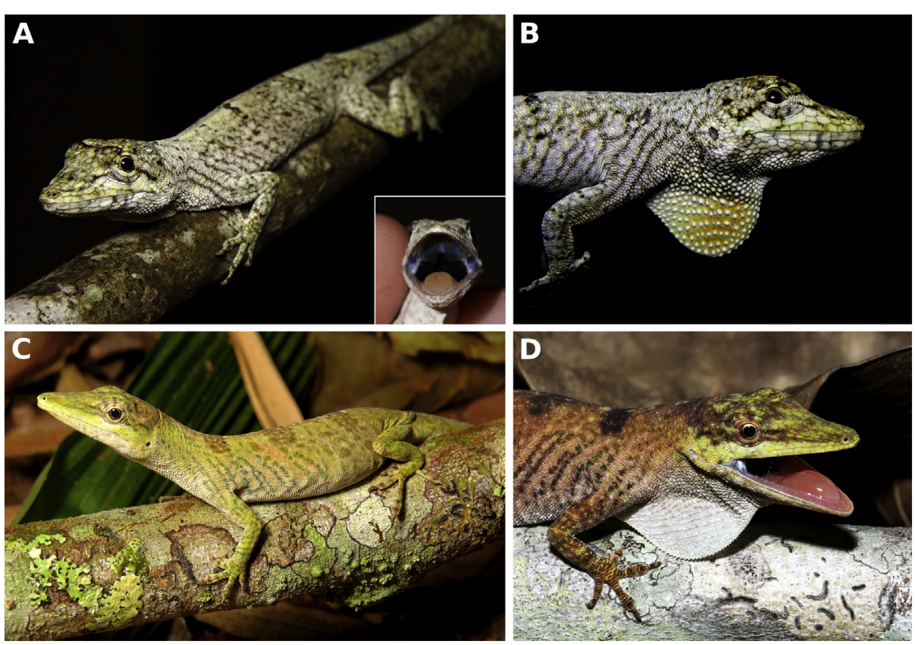

Fig. 1. Coloration in life of *Anolis nasofrontalis* (A, B) and *A. pseudotigrinus* (C, D). In A, inset shows the black throat lining of *A. nasofrontalis*. Photographed specimens are females.