



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.

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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 pre-

dominantly 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

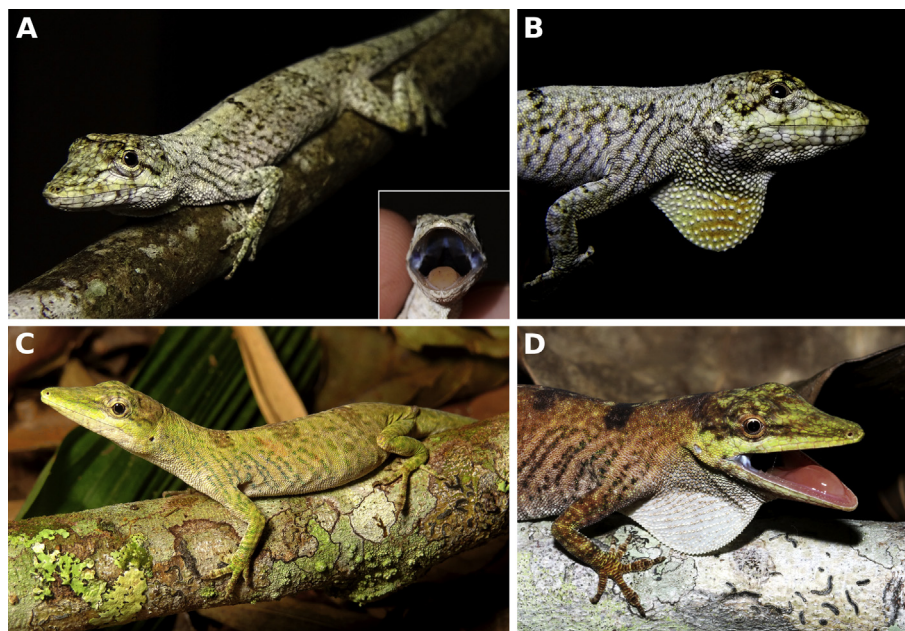


Fig. 1. Coloration in life of *Anolis nasofrontalis* (A, B) and *A. pseudotigrinus* (C, D). In A, inset shows the black throat lining of *A. nasofrontalis*. Photographed specimens are females.

gene *NADH dehydrogenase subunit 2* (ND2) and the flanking *tryptophan transfer RNA* (tRNA-Trp) genes, following Jezkova et al. (2009), as well as the nuclear *recombination-activating gene 1* (RAG1), following Gartner et al. (2013). Mitochondrial sequences obtained in Genbank often included four additional tRNAs flanking the ND2 gene (tRNA-Ala, tRNA-Asx, tRNA-Cys, tRNA-Tyr) (Castañeda and de Queiroz, 2011), which were also used in our final alignments. Sequences were deposited in Genbank (accession numbers MF004396–9). For phylogenetic analyses, we combined our data with sequences generated by Ayala-Varela et al. (2014), Castañeda and de Queiroz (2011), Poe et al. (2015), and Prates et al. (2015), totaling 58 sampled specimens from 56 *Dactyloa* clade *Anolis* species. We also included sequences of *A. fuscoauratus*, *A. ortonii*, *Anolis tandai* Avila-Pires, 1995, and *Anolis trachyderma* Cope, 1876 as outgroups.

Sequences were edited and aligned using Geneious Pro 6 (Biomatters, Auckland). We determined models of nucleotide evolution using Partition Finder 1.1.1 (Lanfear et al., 2012), implementing PhyML for likelihood estimation (Guindon and Gascuel, 2003) and the Bayesian information criterion for model selection (Sullivan and Joyce, 2005). Based on Partition Finder results, codon partitions were implemented for the protein-coding genes. Due to the small size of individual tRNA genes (~70 bp), which impaired proper estimation of substitution parameters in preliminary phylogenetic analyses, these regions were treated as a single partition.

2.2. Inferring phylogenetic relationships and divergence times

We performed simultaneous phylogenetic inference and divergence time estimation for the *Dactyloa* clade of *Anolis* under a Bayesian framework using BEAST 1.8.4 (Drummond et al., 2012). An uncorrelated lognormal relaxed clock (Drummond et al., 2006) was implemented for each locus separately, as well as a birth-death process tree prior (Gernhard, 2008). To improve the estimation of nucleotide substitution rates, we set a lower prior bound of 0.0001 (instead of the default, zero) to the corresponding rate parameters.

In the absence of *Dactyloa* anole fossils for time-calibration, we estimated divergence times through a secondary calibration strategy. For that, we relied on published divergence times among pleurodont iguanian lizards, including four *Dactyloa* species, which were estimated from sequences of five nuclear genes and three well-known fossils as calibration points (Prates et al., 2015). Based on median divergence times and the associated 95% highest posterior density intervals (HPD) provided by Prates et al. (2015), we assigned a normally-distributed calibration prior to the node defining the most recent common ancestor (MRCA) of *Anolis phyllorhinus* Myers and Carvalho, 1945, *A. punctatus*, and *Anolis transversalis* Duméril in Duméril and Duméril, 1851, with a mean of 17.5 million years ago (mya) and a standard deviation of 3.5 mya. Additionally, we set a normally-distributed calibration prior to the node defining the MRCA of those three species and *Anolis dissimilis* Williams, 1965, with a mean of 35.5 mya and standard deviation of 5.5 mya (this latter clade corresponds to the Continenteloa clade of Poe et al., 2015).

To parameterize the mean rate of the molecular clock (ucl.d. mean parameter in BEAST), we relied on substitution rates estimated by a historical demographic study of *Anolis ortonii* and *A. punctatus* (Prates et al., 2016a), which included the loci used in the present investigation. Based on mean mutation rates and the associated HPD from Prates et al. (2016a), we implemented a normally-distributed prior with mean of 1.40×10^{-2} substitutions per site per million year and standard deviation of 5×10^{-3} substitutions per site per million year for the mitochondrial locus (ND2 and flanking tRNAs), and a prior mean of 6.15×10^{-4} , with standard deviation of 1.65×10^{-4} , for the nuclear gene RAG1.

We performed three independent BEAST runs of 50 million generations each, with a sampling frequency of 5000 steps. After assessing convergence and stationarity of model parameters using Tracer 1.6 (available from <http://beast.bio.ed.ac.uk/Tracer>), the three runs were combined in LogCombiner 1.8.4 (with 10% of each run discarded as burn-in). A maximum clade credibility tree was then summarized in TreeAnnotator 1.8.4 (Drummond et al., 2012). Resulting topologies were visualized in FigTree 1.4 (available from <http://tree.bio.ed.ac.uk/software/figtree>).

2.3. Morphological analyses

Morphological measurements and scale characters follow Koehler (2014), with the exception of phalanx terminology, as we consider the concealed ungual phalanx as the first phalanx (following de Queiroz et al., 1998; ungual phalanx not considered in phalanx count by Koehler, 2014). Measurements were made on preserved specimens with a digital caliper to the nearest 0.1 mm. Morphometric measurements are reported for adult specimens only. The scutellation characters of three specimens housed in the Naturhistorisches Museum Wien and one in the Zoologisches Museum Hamburg were scored based on high-resolution images of the head, body and limbs in dorsal, lateral and ventral views. However, no morphometric measurements were made based on photographs. Color in life was extracted from field notes and photographs of recently collected specimens. To support biological inventories in the Atlantic Forest, we provide comparisons of *Anolis nasofrontalis* and *A. pseudotigrinus* with the other native Atlantic Forest anole species (*A. fuscoauratus*, *A. ortonii*, and *A. punctatus*) based on Ávila-Pires (1995).

3. Results

3.1. Phylogenetic relationships and divergence times

Phylogenetic analyses recovered six main clades within *Dactyloa* (Fig. 2), five of which were previously referred to as the *aequatorialis*, *heterodermus*, *latifrons*, *punctatus*, and *roquet* species series (Castañeda and de Queiroz, 2013; Poe et al., 2015; Prates et al., 2015). A sixth clade clustered the newly sampled *Anolis nasofrontalis* and *A. pseudotigrinus* along with *A. dissimilis*, *Anolis calimae* Ayala et al., 1983, *Anolis neblininus* (Myers et al., 1993), and two undescribed Andean species (*Anolis* sp. R and *Anolis* sp. W from Poe et al., 2015). Each of these six major *Dactyloa* clades received maximum support, yet the relationships between them were, generally, poorly supported. The only exception is the well-supported sister relationship between the *aequatorialis* and *latifrons* species series (Fig. 2).

The Atlantic Forest species *Anolis nasofrontalis* and *A. pseudotigrinus* were recovered as sister taxa with high support (Fig. 2). The MRCA of these two anoles is the sister of *A. dissimilis*, a western Amazonian anole from Brazil and Peru. Results indicate that *A. pseudotigrinus* and *A. nasofrontalis* are not close relatives of *A. punctatus*, the only other Atlantic Forest lizard within the *Dactyloa* clade of *Anolis*. Divergence time estimates indicate that *A. pseudotigrinus* and *A. nasofrontalis* share a MRCA at 9.92 mya (HPD = 6.55–13.49 mya; see Supplementary Fig. 1 for HPD of divergences among all taxa), while the MRCA of these two species diverged from its sister *A. dissimilis* around 11.49 mya (HPD = 8–15.36 mya). The MRCA of *A. nasofrontalis*, *A. pseudotigrinus*, *A. dissimilis*, *A. calimae*, and *A. neblininus* was dated as being around 27.14 my old (median value; HPD = 19.96–35.29 mya).

Within the *Dactyloa* clade, divergences between most sampled species predate the Quaternary (i.e., are older than ~2.6 mya), with most such events dating to the Miocene (~5.5–23 mya; Fig. 2). All

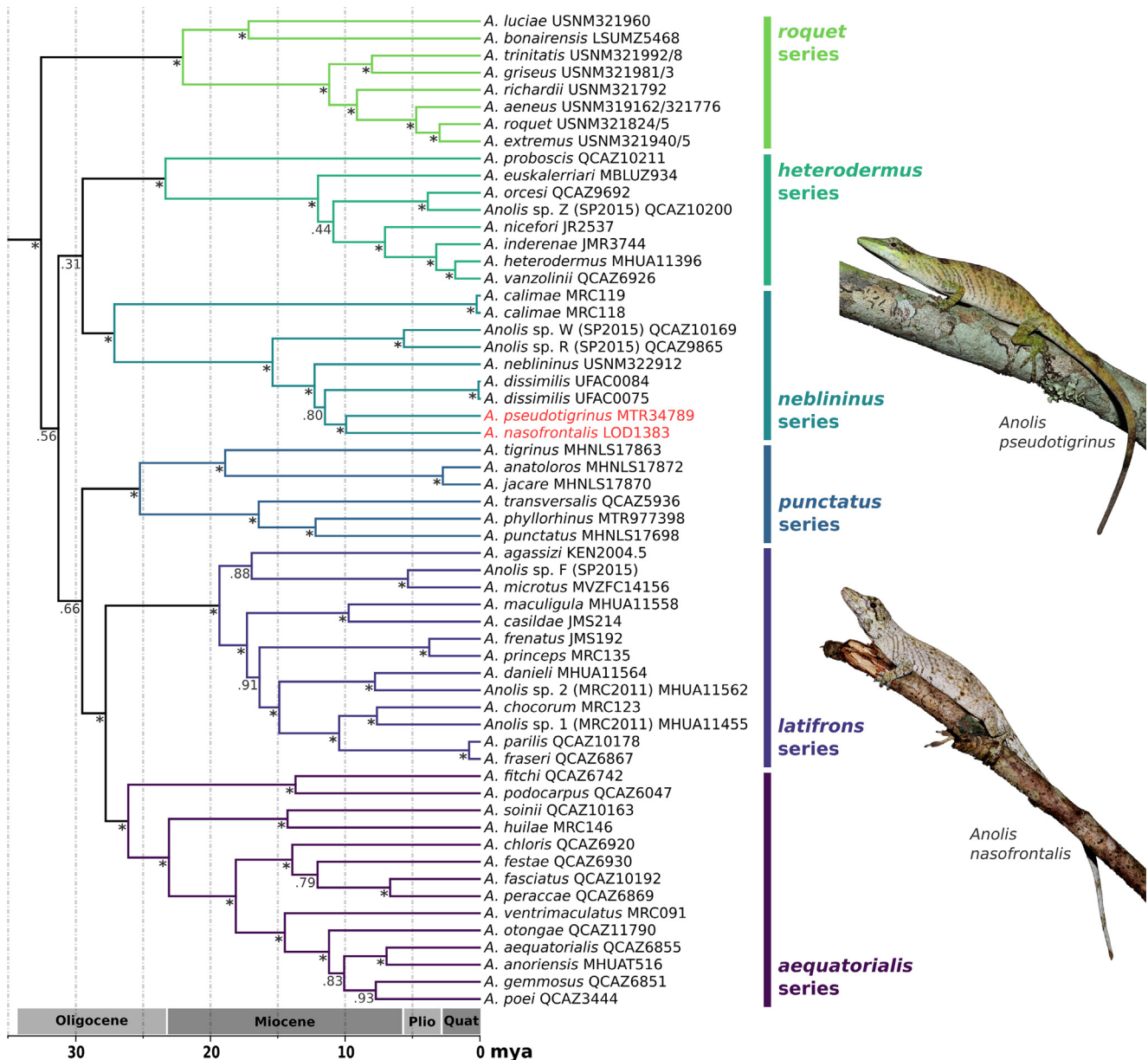


Fig. 2. Phylogenetic relationships and divergence times between species in the *Dactyloa* clade of *Anolis* inferred using BEAST. Asterisks denote posterior probabilities > 0.95.

six major clades within *Dactyloa* began to diversify during the early Miocene and late Oligocene, between 19.33 and 27.14 mya. We found the MRCA of all sampled *Dactyloa* to be 32.58 my old (HPD = 24.59–41.27 mya), while the MRCA of the *Dactyloa* and *Norops* clades of *Anolis* (the latter represented by *A. fuscoauratus*, *A. ortonii*, *A. tandai*, and *A. trachyderma*) was recovered as around 49.31 my old (HPD = 35.72–64.36 mya). Despite the use of different sets of calibrated nodes and the incorporation of a mitochondrial marker in the present study, age estimates for these deeper nodes are very similar to those of Prates et al. (2015).

3.2. Taxonomic accounts

3.2.1. Taxon re-description: *Anolis nasofrontalis* Amaral, 1933

Figs. 1a and b, 2, 3a and b.

Anolis nasofrontalis – Myers and Carvalho, 1945: 6, 9, 14; Williams and Vanzolini, 1980: 99, 103–106; Williams, 1992: 11,

12, 15, 16, 22; Castañeda and de Queiroz, 2013: 350, 375, 379, 380; Poe et al., 2015: 640, 641, 646, 650.

Dactyloa nasofrontalis – Nicholson et al., 2012: 83, 95.

Holotype: MZUSP 440, adult female from Espírito Santo (ES), Brazil, collected by Ernesto Garbe in 1906.

Paratype: MZUSP 440.A, subadult male (the allotype). Same collection data as the holotype. The poor preservation state of this specimen hindered its inclusion in the characterization of *Anolis nasofrontalis*.

Additional specimens examined: ZMH R0411, female from Santa Leopoldina, ES, collected by W. Schlüter on December 1902; NHMW 12742, NHMW 25201.1, and NHMW 25201.2, females from Santa Leopoldina, ES, from the collection of F. Werner (who worked in the Naturhistorisches Museum Wien from 1919 to 1939); MNRJ 1625, adult female from Santa Teresa, ES, collected by A. Ruschi on January 1940; LOD 1383, adult female collected at Reserva Biológica Augusto Ruschi, Santa Teresa, ES, by L.O. Drummond and P.R. Melo-Sampaio on April 2016.

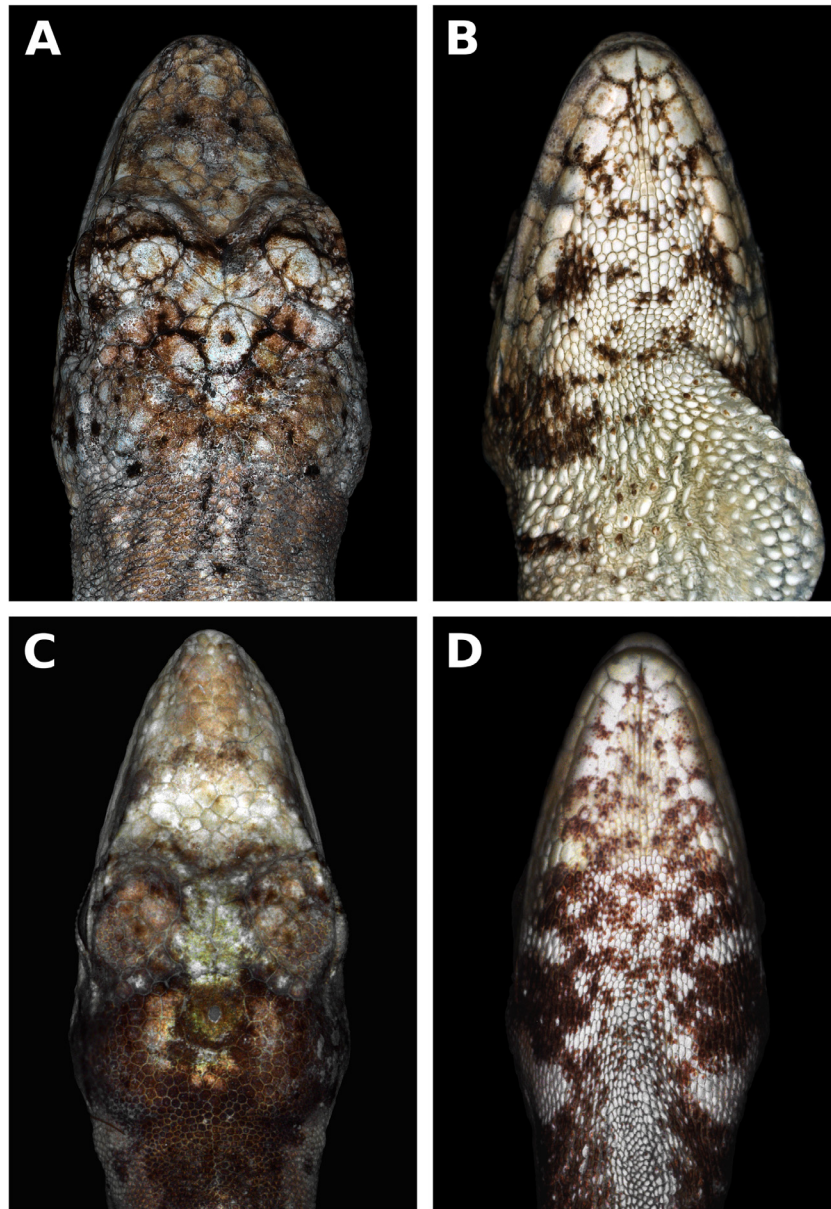


Fig. 3. Head in dorsal and ventral views of *Anolis nasofrontalis* (A, B) and *A. pseudotigrinus* (C, D).

Characterization: Snout-vent length 51.4–55.1 mm; head length 12.8–13.7 mm, width 8.3–8.4 mm; snout length 7–8 mm; ear opening 0.9–1.3 mm horizontally, 0.7 vertically; interparietal scale width 1.4 mm, length 2.2 mm; postcloacal scales not visible in male specimen, likely due to poor preservation; tail length 76.1–85 mm; tail round in cross section; fourth toe of addressed hind limb not reaching posterior insertion of arm; shank length 9.1–10.2 mm; fourth finger of extended forelimb reaching about anterior border of eye; width of dilated subdigital pad 0.9 mm, of non-dilated subdigital pad 0.2 mm.

Dorsal head scales smooth and juxtaposed (Fig. 3a), ventral ones smooth and granular (Fig. 3b); deep prefrontal depression; rostral slightly overlaps mental; four to six postrostrals; single prenasal in contact with rostral; circumnasal in contact with rostral and first supralabial; four to five internasals; six to eight supralabials and five to eight infralabials to the level of center of eye; three to seven postmentals, the two outer ones greatly enlarged; two to five enlarged sublabials in contact with infralabials; canthal ridge indistinct to well-defined; eight to 17 smooth loreals in two to four

rows at level of second canthal; five to seven scales between first canthals, four to seven between second canthals; three to four smooth suboculars in a single row, in contact with supralabials; one to three slightly elongated smooth superciliaries above anterior portion of eye; two to three greatly enlarged smooth supraoculars; one incomplete row of circumorbitals separating supraoculars from supraorbital semicircles; semicircles broadly in contact; parietal depression shallow to moderate; interparietal distinctly enlarged, surrounded by large to moderate-sized scales; scales anterior and posterior to ear opening subequal, slightly larger anteriorly.

Dewlap small in males and females; anterior insertion of dewlap at level of posterior border of eye, posterior insertion at level of anterior insertion of arm; about five to seven rows of gorgetal-sternal dewlap scales, about twice as large as ventrals, separated by naked skin.

Dorsal body scales smooth and juxtaposed, mostly hexagonal; no enlarged rows of dorsals; 78–89 dorsals longitudinally between

level of axilla and groin; lateral scales smooth, granular, rounded; ventrals smooth, imbricate, with rounded posterior margins, about twice the size of dorsals; 66–73 ventrals longitudinally between level of axilla and groin; 95–104 scales around mid-body; axillary depression or pocket absent; proximal portion of tail (about 1/5 of tail length) with smooth, mostly hexagonal scales, distal portion with keeled, imbricate, mostly hexagonal scales.

Supradigital scales smooth; 27–32 subdigital lamellae under phalanges III–V of fourth toe, six to seven scales under second phalanx; ventral surface of second phalanx raised relative to that of proximal phalanges; subdigital lamellae of toepad projecting distally under subdigital scales of second phalanx.

Color in life: Dorsal surface of body, tail and limbs lichenous with light-gray background (Fig. 1a and b); diagonal lines composed of dark-brown spots on first half of body, irregularly-distributed dark reticulations and scattered yellow spots on second half; a dark and well-marked interorbital line on the dorsal surface of head; two dark lines radiating from each eye, first one extending posteriorly halfway to tympanum, second anteriorly through canthus rostralis; iris brown; tail with nine dark-brown bands; ventral surface of head, body, tail and limbs light-gray with scattered dark-brown spots; throat lining black (Fig. 1a); tongue tan; female dewlap skin light-orange, faded to white posteriorly; dewlap scales white; based on Amaral (1933), male dewlap skin pink.

Species comparisons (traits of taxa compared to *Anolis nasofrontalis* in parentheses): *A. nasofrontalis* can be distinguished from *A. fuscoauratus*, *A. ortonii*, and *A. punctatus* by 95–104 scales around mid-body (*A. fuscoauratus*: 124–157; *A. ortonii*: 123–180; *A. punctatus*: 132–167), smooth dorsals (weakly keeled), and smooth snout scales between nostrils (keeled). *Anolis nasofrontalis* further differs from *A. fuscoauratus* and *A. punctatus* by a lichenous dorsal body coloration (*A. fuscoauratus*: brown or gray; *A. punctatus*: green, often with white spots), supraorbital semicircles in contact (separated by granular scales) and well-developed dewlap in females (vestigial). *Anolis nasofrontalis* can be distinguished from *A. pseudotigrinus* by about five to seven rows of gorgetal-sternal dewlap scales (12–14), 78–89 dorsals (87–98) and 66–73 ventrals (79–90) between axilla and groin, 95–104 scales around mid-body (106–118), and a small light orange dewlap in females (large white dewlap). *Anolis nasofrontalis* can be further distinguished from *A. pseudotigrinus* and *A. punctatus* by a blunt snout (pointed).

Distribution and natural history: *Anolis nasofrontalis* is presently confirmed to occur in the Reserva Biológica Augusto Ruschi in Santa Teresa, ES, at an altitude of 745 m above sea level (asl). Local vegetation is characterized by dense broad-leaf montane Atlantic rainforest. The recently-collected specimen was found sleeping at night on a narrow branch at a height of about 3 m. This species is sympatric with *A. fuscoauratus*, *A. pseudotigrinus*, and *A. punctatus*. Four additional *A. nasofrontalis* (housed in Vienna and Hamburg) were identified as collected in Santa Leopoldina, ES, a lowland site (~85 m asl) situated about 18 km away from Santa Teresa; yet, this name was previously used to designate a municipality of large territorial extent that was dismembered into smaller districts, including the Comuna de Santa Teresa (currently the municipality of Santa Teresa). We failed to find *A. nasofrontalis* in Santa Leopoldina; its presence in this area is yet to be confirmed.

3.2.2. Taxon re-description: *Anolis pseudotigrinus* Amaral, 1933

Figs. 1c and d, 2, 3c and d.

Anolis pseudotigrinus – Myers and Carvalho, 1945: 6; Williams and Vanzolini, 1980: 99, 103–106; Williams, 1992: 11, 12, 15, 16, 22; Castañeda and de Queiroz, 2013: 350, 375, 379, 380; Poe et al., 2015: 640, 641, 646, 650.

Dactyloa pseudotigrina – Nicholson et al., 2012: 83, 96.

Holotype: MZUSP 721.B, adult female from the Rio Doce region, ES, collected by Ernesto Garbe in 1906.

Additional specimens examined: MZUSP 36718, adult male collected in Santa Teresa, ES, by J. F. Jackson on February 1974; MBML 327, adult female, MBML 266 and 536, two adult males, and MBML 554, subadult male, all collected in the park of the Museu de Biologia Professor Melo Leitão in Santa Teresa, by M.G. Hoffmann in 1997–8; MTR 34789 and 34790, two adult females collected in the Reserva Biológica Augusto Ruschi, ES, by M. Teixeira Jr., M.T. Rodrigues, F. Dal Vechio, R.S. Recoder and R. Damasceno on December 2014; LOD 1237, subadult female from Reserva Biológica Augusto Ruschi, collected by L.O. Drummond and P.R. Melo-Sampaio on February 2016.

Characterization: Snout-vent length 56.4–65.8 mm; head length 15.4–17.2 mm, width 7.2–8.1 mm; snout length 8.4–9.8 mm; ear opening 0.7–1.0 mm horizontally, 0.8–1 mm vertically; interparietal scale width 1.9–2.4 mm, length 2.3–2.7 mm; postcloacal scale width in males 0.6–1.3 mm; tail length 101–112 mm; tail round in cross section; fourth toe of adpressed limb reaching posterior insertion of arm; shank length 10.2–11.1 mm; fourth finger of extended forelimb reaching about anterior border of eye; width of dilated subdigital pad 1.2–1.5 mm, of non-dilated subdigital pad 0.3–0.4 mm.

Dorsal head scales smooth and juxtaposed (Fig. 3c), ventral ones smooth and granular (Fig. 3d); deep prefrontal depression; rostral strongly overlaps mental; four to seven postrostrals; one to two prenasals, lower one in contact with rostral; circumnasal in contact with rostral and first supralabial; four to six internasals; seven to nine supralabials and infralabials to the level of center of eye; four to five postmentals, the two outer ones greatly enlarged; two to four enlarged sublabials in contact with infralabials; canthal ridge indistinct; 16–24 smooth loreals in three to five rows at level of second canthal; six to seven scales between first canthals, five to seven between second canthals; four to five smooth suboculars in a single row, in contact with supralabials; one to two smooth to keeled elongate superciliaries above anterior portion of eye; two to five greatly enlarged smooth supraoculars; one incomplete row of circumorbitals separating supraoculars from supraorbital semicircles; semicircles broadly in contact; parietal depression ill-defined; interparietal distinctly enlarged, surrounded by large to moderate-sized scales; semicircles in contact with interparietal, or separated by one scale; scales anterior and posterior to ear opening subequal to slightly larger anteriorly.

Dewlap large in males and females; anterior insertion of dewlap at level of anterior border of eye, posterior insertion at level of posterior insertion of arm (females) or reaching about 1/3–1/2 of length between axilla and groin (males); about 12–14 rows of gorgetal-sternal dewlap scales, about twice as large as ventrals, separated by naked skin.

Dorsal body scales smooth, juxtaposed, mostly hexagonal; no enlarged rows of dorsals; 87–98 dorsals longitudinally between level of axilla and groin; lateral scales smooth, granular, rounded; ventrals smooth, imbricate, with rounded posterior margins, about twice the size of dorsals; 79–90 ventrals longitudinally between level of axilla and groin; about 106–118 scales around mid-body; axillary depression or pocket absent; proximal portion of tail (about 1/4–1/5 of tail length) with smooth, mostly hexagonal scales, distal portion with keeled, imbricate, mostly hexagonal scales; in males, two moderately enlarged postcloacals.

Supradigital scales smooth; 26–30 subdigital lamellae under phalanges III–V of fourth toe, six to seven scales under second phalanx; ventral surface of second phalanx raised relative to that of proximal phalanges; subdigital lamellae of toepad projecting distally under subdigital scales of second phalanx.

Color in life: Dorsal surface of body, tail and limbs lichenous with light-green to olive-green background (Fig. 1c and d); diagonal lines composed of dark-green or bluish spots on first half of body, irregularly-distributed green reticulations and green spots

on second half; dorsal surface of head green; large brown nuchal spot; no dark interorbital line; iris brown; four large mid-dorsal brown spots on body, first at level of anterior limb insertion, fourth at level of posterior limb insertion; tail with four to six brown spots or bands; ventral surface of head, body, tail, and limbs light-gray with scattered dark-brown spots; throat lining black; tongue pink; female dewlap skin white; dewlap scales white; male dewlap coloration unknown.

Species comparisons (traits of taxa compared to Anolis pseudotigrinus in parentheses): *Anolis pseudotigrinus* can be distinguished from *A. fuscoauratus*, *A. ortonii*, and *A. punctatus* by a lichenous dorsal body coloration with green background (*A. fuscoauratus*: brown or gray; *A. ortonii*: marmorated with brown, gray and black; *A. punctatus*: green, often with white spots), 106–118 scales around mid-body (*A. fuscoauratus*: 124–157; *A. ortonii*: 123–180; *A. punctatus*: 132–167), smooth dorsals (weakly keeled), and smooth snout scales between nostrils (keeled). *Anolis pseudotigrinus* further differs from *A. fuscoauratus* and *A. punctatus* by supraorbital semi-circles in contact (separated by granular scales) and well-developed dewlap in females (vestigial). *Anolis pseudotigrinus* differs from *A. nasofrontalis* by about 12–14 rows of gorgetal-sternal dewlap scales (five to seven), 87–98 dorsals (78–89) and 79–90 ventrals (66–73) between axilla and groin, 106–118 scales around mid-body (95–104), and large white dewlap in females (small orange dewlap). *Anolis pseudotigrinus* can be further distinguished from *A. fuscoauratus*, *A. nasofrontalis*, and *A. ortonii* by a pointed snout (blunt).

Distribution and natural history: *Anolis pseudotigrinus* is known only from the Reserva Biológica Augusto Ruschi (~745 m asl) and from the forest reserve of the Museu de Biologia Professor Melo Leitão (~700 m asl), both in Santa Teresa, ES. It is sympatric with *A. fuscoauratus*, *A. nasofrontalis* and *A. punctatus*. The local vegetation is characterized by dense broad-leaf montane Atlantic rainforest. Specimens were collected during the night, sleeping on narrow branches at a height of 2–3 m, one of them on a bamboo cluster near forest edge.

4. Discussion

4.1. Phylogenetic relationships and taxonomic implications

Historical relationships among South American anoles have been controversial, yet much improved by genetic data, which have revealed unexpected phylogenetic and biogeographic associations (e.g., Castañeda and de Queiroz, 2011; Nicholson, 2002; Nicholson et al., 2005; Poe, 2004; Prates et al., 2015). Traditionally, *Anolis nasofrontalis* and *A. pseudotigrinus* have been assigned to the *tigrinus* species group, which also included species from the Colombian and Venezuelan Andes (Williams, 1976, 1992). Because molecular data recovered the *tigrinus* group as partially nested within the *punctatus* species series, that group designation is no longer used (Castañeda and de Queiroz, 2011). Subsequently, *A. nasofrontalis* and *A. pseudotigrinus* were tentatively assigned to the *punctatus* species group (Nicholson et al., 2012), and, more recently, considered *incertae sedis* within *Dactyloa* due to poor resolution in phylogenetic analyses that incorporated both genetic and morphological data (Castañeda and de Queiroz, 2013; Poe et al., 2015). Based on new DNA sequence data, we were able to refine the phylogenetic placement of these two poorly-known Brazilian species.

New genetic data from *Anolis nasofrontalis* and *A. pseudotigrinus* have implications for *Dactyloa* anole taxonomy. Similar to our study, previous molecular phylogenetic analyses found *A. neblininus* and *A. calimae* (Castañeda and de Queiroz, 2011), or these two species along with *A. dissimilis* (Prates et al., 2015), to compose

a clade within *Dactyloa*. This clade fell outside of the *aequatorialis*, *heterodermus*, *latifrons*, *punctatus*, and *roquet* species series (Castañeda and de Queiroz, 2013; Poe et al., 2015), suggesting a sixth major *Dactyloa* clade. In agreement with this scenario, our analyses found *A. nasofrontalis*, *A. pseudotigrinus*, *A. calimae*, *A. dissimilis*, *A. neblininus*, and two undescribed Andean species (*Anolis* sp. R and *Anolis* sp. W from Poe et al., 2015) to compose an exclusive clade. In the face of these findings, and for practical reasons, we define a sixth species series within the *Dactyloa* clade of *Anolis*: the *neblininus* species series. It is named after the *neblininus* group of Williams et al. (1996), composed by the Guiana Shield endemics *A. neblininus* and *Anolis carlostoddi* (Williams et al., 1996) and formerly allocated to the genus *Phenacosaurus* Lazell, 1969 (a genus later synonymized with *Anolis*; Poe, 1998). The *neblininus* species series is composed of all extant *Dactyloa* anole species more closely related to *A. neblininus* than to *Anolis aequatorialis* Werner, 1894, *Anolis heterodermus* Duméril in Duméril and Duméril, 1851, *Anolis latifrons* Berthold, 1846, *A. punctatus*, and *Anolis roquet* Bonnatere, 1789. Its inferred composition includes *A. calimae*, *A. dissimilis*, *A. nasofrontalis*, *A. neblininus*, and *A. pseudotigrinus* based on our phylogenetic results, as well as *A. carlostoddi* in accordance with Williams et al. (1996).

Further sampling of South American anole taxa may reveal additional members of the *neblininus* species series, perhaps with implications for the phylogenetic affinities of *Anolis nasofrontalis* and *A. pseudotigrinus*. For instance, these two species share with the central Andean *Anolis williamsmittermeierorum* Poe and Yañez-Miranda, 2007 a black throat lining, a seemingly unusual trait (Poe and Yañez-Miranda, 2007) that may be indicative of close phylogenetic relationships. In a study incorporating both molecular and morphological characters (Poe et al., 2015), *A. williamsmittermeierorum* and its relative *Anolis peruensis* Poe, Latella, Ayala-Varela, Yañez-Miranda and Torres-Carvajal, 2015 were found to be closely related to *A. neblininus*, a close relative of *A. nasofrontalis* and *A. pseudotigrinus* in our analysis. Poe et al. (2015) also found *A. peruensis* and *A. williamsmittermeierorum* to be closely related to *A. carlostoddi*, a member of Williams' former *neblininus* group, and to *Anolis bellipeniculus* (Myers and Donnelly, 1996), another *tepui* (table mountain) endemic. Based on these findings, we expect that the *neblininus* series will likely expand to include Andean and Guiana Shield species for which genetic data is not yet available, as well as still unnamed anoles such as *Anolis* sp. R and *Anolis* sp. W (Poe et al., 2015).

Along with other members of the *neblininus* species series, *Anolis nasofrontalis* and *A. pseudotigrinus* exhibit morphological attributes that have been associated with the Greater Antillean “twig anole” ecomorph, such as short limbs and cryptic coloration (Williams, 1976, 1992). This twig anole-like morphology has been also attributed to Andean anoles currently assigned to the *punctatus* (e.g., *Anolis tigrinus* Peters, 1863) and *heterodermus* series (e.g., *Anolis euskalerriari* (Barros et al., 1996), *Anolis orcesi* (Lazell, 1969), and *Anolis proboscis* Peters and Orces, 1956) (Losos et al., 2012; Poe et al., 2015; Williams et al., 1996). Phylogenetic relationships within *Dactyloa* support the view of recurrent evolution of a twig anole-like phenotype in South America, perhaps as a result of adaptive convergence; alternatively, this pattern may reflect the conservation of a phenotype ancestral for the *Dactyloa* clade (Castañeda and de Queiroz, 2011; Poe et al., 2015). In the former case, an apparent association with South American mountains is intriguing. Nevertheless, natural history data are still needed to assess whether mainland anoles exhibit the typical ecological and behavioral traits that characterize Caribbean anole ecomorphs – in the case of twig anoles, active foraging, slow movements, infrequent running or jumping, and preference for narrow perching surfaces (Losos, 2009). Although scarce, the available data support that at least some twig anole-like mainland species behave as

typical Caribbean twig anoles, as is the case of *Anolis proboscis* (Losos et al., 2012).

4.2. Biogeographic connections between South American highlands

Species in the *neblininus* series have been sampled in localities separated by large geographic distances (Fig. 4). While *Anolis nasofrontalis* and *A. pseudotigrinus* are restricted to the southern montane Atlantic Forest, *A. dissimilis* is known from a few sites in southwestern Amazonia adjacent to the Andean foothills, *A. calimae* occurs on the western cordillera of the Colombian Andes, and *A. neblininus* is a narrow tepui endemic in the Guiana Shield, close to the Brazil–Venezuela border. Such purported relationships point to an assortment of narrowly-distributed mainland anoles that are associated with mid elevations, or their adjacent habitats in the case of *A. dissimilis* (Fig. 4). A similar pattern has been found by a number of phylogenetic studies of South American frog clades (e.g., Castroviejo-Fisher et al., 2014, 2015; Fouquet et al., 2012a,b; Padial et al., 2014).

Close phylogenetic relationships between these highly disjunct and narrowly distributed lizards seem to indicate a complex biogeographic history involving former patches of suitable habitat between regions, followed by habitat retraction and extinction in the intervening areas. In the case of *Anolis nasofrontalis* and *A. pseudotigrinus*, past forest corridors may explain a close relationship with the western Amazonian *A. dissimilis*. Atlantic and Amazonian rainforests are presently separated by the open savannas and

shrublands of the Caatinga, Cerrado and Chaco domains. However, geochemical records suggest that pulses of increased precipitation and wet forest expansion during the Quaternary have favored intermittent connections between western Amazonia and the southern Atlantic Forest (through present-day southwestern Brazil), as well as between eastern Amazonia and the northern Atlantic Forest (through northeastern Brazil) (Cheng et al., 2013). Genetic data indicate that a northern forest connection has led to colonization of the Atlantic Forest from eastern Amazonia by *A. ortonii* and *A. punctatus*, as well as by the bush anole *Polychrus marmoratus* (Linnaeus, 1758), in the mid-Pleistocene (Prates et al., 2016a). By contrast, our findings indicate a much older, Miocene divergence between *A. dissimilis* and the ancestor of *A. nasofrontalis* and *A. pseudotigrinus*. Similar to our results, Miocene divergences between disjunct sister species and clades that occur in southern Atlantic Forest and western Amazonia have been reported for a number of bird and frog taxa (e.g., Batalha-Filho et al., 2013; Gehara et al., 2014). These old divergences suggest that intermittent southern forest connections in South America may largely pre-date the time frame encompassed by most available paleoenvironmental data (i.e., the Pleistocene; Cheng et al., 2013).

These inferred biogeographic connections in South America may have also been influenced by major landscape shifts as a result of Andean orogeny during the mid to late Miocene. The timing of divergence between *Anolis dissimilis* and the ancestor of *A. nasofrontalis* and *A. pseudotigrinus* (~11.5 mya) overlaps with that of the Chapare butress (Fig. 4), which was a land bridge that connected the central Andes to the western edge of the Brazilian

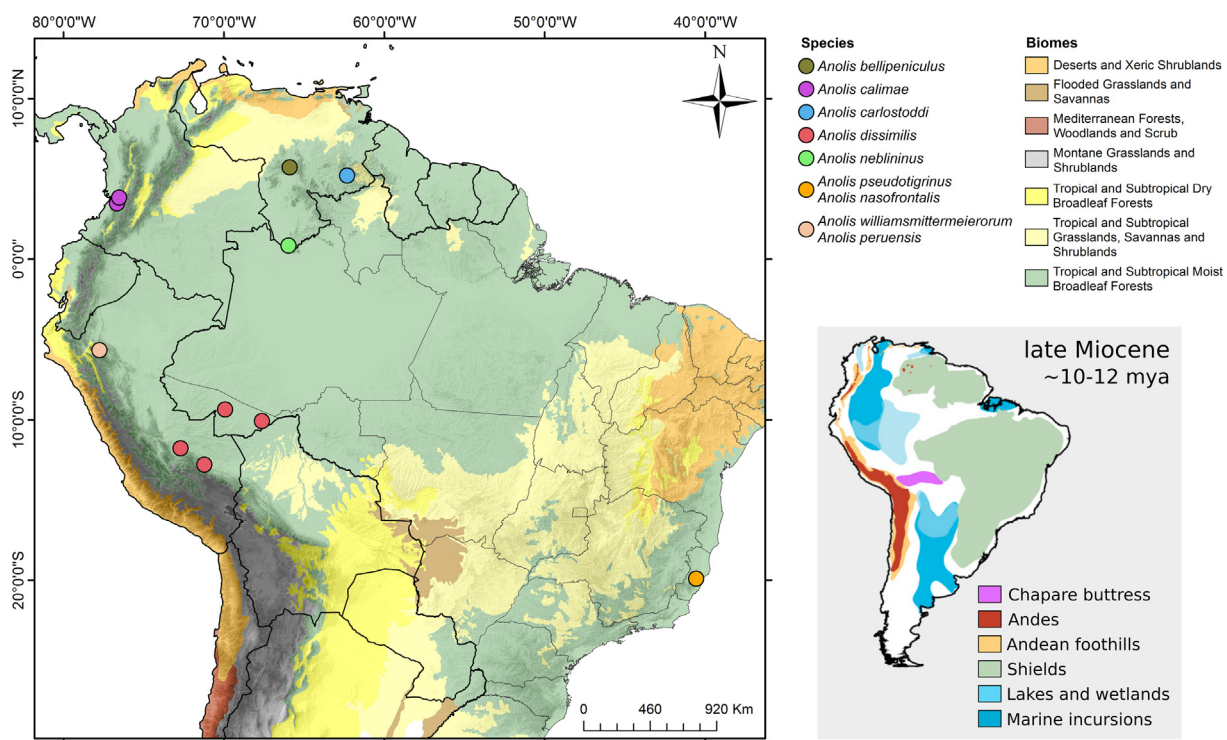


Fig. 4. Geographic distribution of confirmed and purported members of the *neblininus* species series within the *Dactyloa* clade of *Anolis*. *Anolis bellipeniculus*: Cerro Yaví, Amazonas, Venezuela (Myers and Donnelly, 1996); *A. calimae*: San Antonio, Television Tower Mountain, Valle del Cauca, Colombia, and Lake Calima Dam, Darién, Valle del Cauca, Colombia (Ayala et al., 1983); *A. carlostoddi*: Abacapa-tepui, Chimantá massif, Bolívar, Venezuela (Williams et al., 1996); *A. dissimilis*: Fazenda Experimental Catuaba, Senador Guimard, Acre, Brazil (Melo-Sampaio et al., 2013; Prates et al., 2015), Parque Estadual Chandless, Manoel Urbano, Acre, Brazil (Freitas et al., 2013), San Martín, Lower Urubamba Region, Peru (Icochea et al., 2001), and Itahuania, upper Rio Madre de Dios, Madre de Dios, Peru (Williams, 1965); *Anolis nasofrontalis* and *A. pseudotigrinus*: Santa Teresa, Espírito Santo, Brazil (this study; Myers and Carvalho, 1945; Williams and Vanzolini, 1980); *A. neblininus*: Cerro de la Neblina, Amazonas, Venezuela (Myers et al., 1993); *A. peruensis*: Esperanza, Amazonas, Peru (Poe et al., 2015); *A. williamsmittermeierorum*: Venceremos, San Martín, Peru (Poe and Yañez-Miranda, 2007). For the last two taxa, a single point is depicted on map due to close proximity of collection sites. The inset presents a schematic map of South America around 10–12 mya (based on Lundberg et al., 1998), illustrating the approximate locality of the Chapare butress, a land bridge that connected the central Andes to the western edge of the Brazilian Shield during the Miocene.

Shield, around present-day Bolivia (Lundberg et al., 1998). This bridge may have acted as a path for west-east movement of terrestrial organisms isolated by the paleo-Amazonas (to the north) and Paraná (to the south) river systems, and later by the Pebasian and Paranan inland seas (Wesselingh and Salo, 2006). Additionally, wet environments associated with the Paraná system may have acted as a corridor between this region and Brazil's southeast (Batalha-Filho et al., 2013), favoring biotic exchange between the southern Atlantic Forest with the Andean Yungas and adjacent western Amazonia. Although unconfirmed, the historical records of *A. nasofrontalis* in a lowland site (Santa Leopoldina) may indicate some tolerance to lowland conditions in this group of anoles, in agreement with the presence of the closely-related *A. dissimilis* in lowland western Amazonia. Such tolerance may have played a role in the colonization of the Atlantic Forest from western South America, through occupation of the intervening lowlands.

Interestingly, geological evidence also supports connections between the northern Andes and the Guiana Shield during the mid-Miocene through the Vaupés Arch (Lundberg et al., 1998), which is consistent with our divergence time estimates between Andean and Guianan highland anoles from the *neblininus* species series.

4.3. Concluding remarks

Building upon the valuable molecular scaffolding first provided by Castañeda and de Queiroz (2011) for the *Dactyloa* clade of *Anolis*, our knowledge about this group's diversity and evolution has increased rapidly. Based on new biological inventories and genetic data, we have uncovered the phylogenetic relationships and provided a taxonomic re-description of *A. nasofrontalis* and *A. pseudotigrinus*, two rare endemic Atlantic Forest anoles. We find evidence of a Miocene rainforest corridor between southeastern Brazilian forests and western Amazonia, and biogeographic associations with similarly narrowly-distributed species from the Andes and the Guiana Shield. Based on the phylogenetic results, we define the *neblininus* species series, a sixth major clade within the *Dactyloa* radiation of *Anolis*.

It has become increasingly clear that broader sampling of genetic variation is essential in advancing studies of mainland anole taxonomy and evolution. This significant challenge also provides exciting opportunities for complementary sampling efforts, exchange of information, and new collaborations between research groups working in different South American countries.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2017.05.009>.

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