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Discovery of a new species of *Anolis* lizards from Brazil and its implications for the historical biogeography of montane Atlantic Forest endemics

Ivan Prates^{1,*}, Paulo Roberto Melo-Sampaio², Kevin de Queiroz¹, Ana Carolina Carnaval³, Miguel Trefaut Rodrigues⁴, Leandro de Oliveira Drummond⁵

Abstract. Recent biological discoveries have changed our understanding of the distribution and evolution of neotropical biotas. In the Brazilian Atlantic Forest, the discovery of closely related species isolated on distant mountains has led to the hypothesis that the ancestors of montane species occupied and dispersed through lowland regions during colder periods. This process may explain the distribution of an undescribed *Anolis* lizard species that we recently discovered at a montane site in the Serra dos Órgãos National Park, a popular tourist destination close to the city of Rio de Janeiro. To investigate whether this species is closely related to other Atlantic Forest montane anoles, we implement phylogenetic analyses and divergence time estimation based on molecular data. We infer the new species nested within the *Dactyloa* clade of *Anolis*, forming a clade with *A. nasofrontalis* and *A. pseudotigrinus*, two species restricted to montane sites about 400 km northeast of Serra dos Órgãos. The new species diverged from its sister *A. nasofrontalis* around 5.24 mya, suggesting a cold-adapted lowland ancestor during the early Pliocene. Based on the phylogenetic results, we emend the definitions of the series taxa within *Dactyloa*, recognizing a clade containing the new species and several of its relatives as the *nasofrontalis* series. Lastly, we provide morphological data supporting the recognition of the new species and give it a formal scientific name. Future studies are necessary to assess how park visitors, pollutants, and shrinking montane habitats due to climate change will affect this previously overlooked anole species.

Keywords: *Anolis neglectus* sp. nov., *Dactyloa*, mainland, phylogeny, systematics, taxonomy.

Introduction

Recent biological discoveries have transformed our understanding of the distribution and evolution of neotropical biotas (Mahler et al., 2016; Prates et al., 2017). These discoveries often come from well-studied regions, as is the case of the Atlantic Forest, a highly threatened biodiversity hotspot in eastern Brazil. The Atlantic

Forest region arguably harbors the largest concentration of universities and research centers in South America, and its fauna has therefore been extensively studied (Moura et al., 2018). Nevertheless, the recent rediscovery of reptile and amphibian species that have been undetected for decades (e.g., Prates et al., 2017; Rodrigues et al., 2009) and the frequent discovery of new species (e.g., Rodrigues et al., 2013; Costa et al., 2015; Graboski et al., 2015) and higher taxa (e.g., Rodrigues et al., 2005, 2007, 2009) highlight our still limited understanding of the regional fauna.

By outlining species ranges and providing genetic samples, biological surveys in the Atlantic Forest have shed light on the history of South American habitats (Carnaval et al., 2009, 2014; Dal-Vechio et al., 2018). Molecular investigations of *Anolis* lizards, a clade composed of more than 400 extant species in the Americas

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(Uetz, 2019), have revealed that species interchange between the Atlantic Forest and Amazonia was essential for the assembly of current biotas, challenging a simple scenario of in situ diversification (Prates et al., 2015, 2016a, b, 2017, 2018). Emerging biogeographic patterns in mainland anoles illustrate how studies of the origins of tropical biodiversity depend on adequate knowledge about species distributions and evolutionary relationships.

Five native and two introduced species of *Anolis* inhabit the Atlantic Forest. The non-native species, *Anolis sagrei* Duméril and Bibron, 1837 and *Anolis porcatus* Gray, 1840, likely represent recent introductions (Prates et al., 2016c; Oliveira et al., 2018). Among the native species, three have broad distributions in lowland Atlantic Forest and Amazonia: *Anolis punctatus* Daudin, 1802, a member of *Dactyloa* clade within *Anolis* (sensu Poe et al., 2017), and *Anolis fuscoauratus* D'Orbigny in Duméril and Bibron, 1837 and *Anolis ortonii* Cope, 1868, both in the nested *Digilimbus*, *Norops*, and *Draconura* clades (Poe et al., 2017). The other two Atlantic Forest anole species are endemic to montane areas in Brazil's southeast: *Anolis nasofrontalis* Amaral 1933 and *Anolis pseudotigrinus* Amaral 1933, both in *Dactyloa*. These two montane anoles went undetected for more than 40 years following their original descriptions (Prates et al., 2017), possibly as a result of their cryptic coloration and habits. *Anolis nasofrontalis* and *A. pseudotigrinus* were the last new anoles described from the Atlantic Forest region since their collection by Ernest Garbe in 1906.

Recent molecular analyses found that *A. nasofrontalis* and *A. pseudotigrinus* are closely related to anole lizards that occur in the Andes and highland habitats in the Guiana Shield (Prates et al., 2017). This pattern suggests that the ancestors of montane species occupied and dispersed through lowland regions during colder times, becoming isolated on mountains when temperatures increased (Firkowski et al., 2016).

This process may also explain the distribution of an undescribed anole species (fig. 1) that we recently discovered in the Serra dos Órgãos National Park, a popular tourist destination and well-studied conservation unit close to the city of Rio de Janeiro. The new species is morphologically similar to *A. nasofrontalis* and *A. pseudotigrinus*, known from mountains situated about 400 km northeast of Serra dos Órgãos (fig. 2). In this contribution, we investigate the relationships of this newly discovered anole species to the two other highland Atlantic Forest *Anolis* species and other members of the *Dactyloa* clade, including estimates of their divergence times. We also provide morphological data supporting the recognition of the new species, and we give it a formal scientific name.

Material and methods

Sampling of molecular data

Individuals were euthanized in the field with an intraperitoneal injection of tricaine methanesulfonate (approved by the City College of New York Institutional Animal Care and Use Committee, protocol no. 993), fixed in 10% formalin for 24 hours, and transferred to 70% ethanol for permanent storage. Liver samples were taken prior to fixation and stored in absolute ethanol for molecular analyses. Genomic DNA was extracted from liver fragments following Prates et al. (2018).

For molecular phylogenetic inference, we matched data available in GenBank by sequencing the mitochondrial gene *NADH dehydrogenase subunit 2* (ND2) and the flanking *tryptophan transfer RNA* (tRNA-Trp) genes, using primers and PCR conditions provided by Jezkova, Leal, Rodriguez-Robles (2009); as well as the nuclear *recombination-activating gene 1* (RAG1), following Gartner et al. (2013). Sanger sequencing was performed by Macrogen USA (New York, NY). Newly generated sequences from two individuals of the new species were deposited in GenBank (accession numbers MK726355, MK726356, MK733621, MK733622). We combined these data with sequences generated by Castañeda and de Queiroz (2011), Ayala-Varela et al. (2014), Poe et al. (2015, 2017), Prates et al. (2015, 2017), and Torres-Carvajal et al. (2018). Most ND2 + tRNA-Trp sequences obtained from GenBank included up to four additional tRNAs flanking the ND2 gene (tRNA-Ala, tRNA-Asn, tRNA-Cys, tRNA-Tyr), which were also included in our final alignments. To improve phylogenetic inference, we also incorporated sequences of the *cytochrome oxidase I* gene (COI) given its broad availability for *Dactyloa* clade

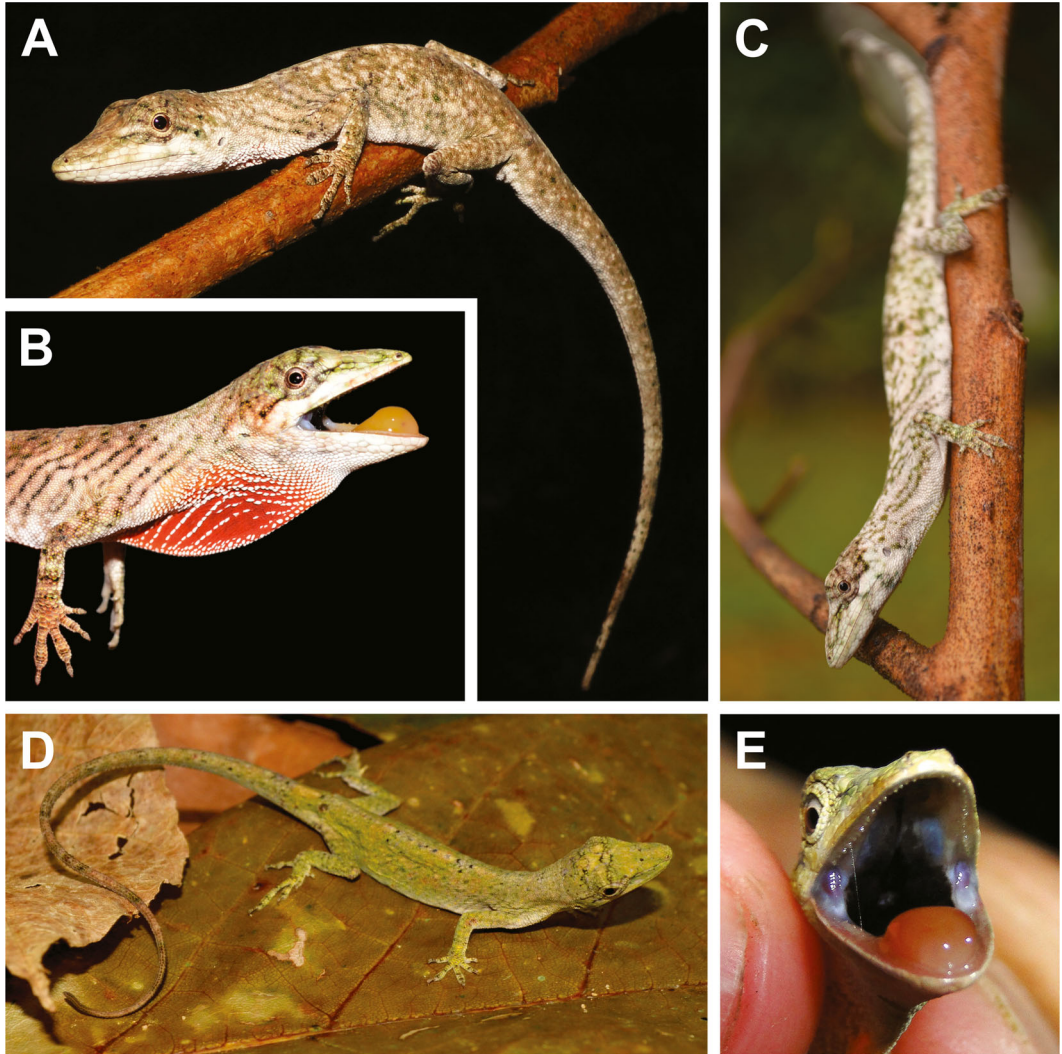


Figure 1. *Anolis neglectus*, sp. nov. in life. (A) Male paratype MNRJ 26930 (SVL 51.4 mm). (B) Male holotype MNRJ 26927 (SVL 53.3 mm). (C) Female paratype MNRJ 26931 (SVL 62.7 mm). (D) Female paratype MNRJ 26928 (SVL 54 mm). (E) Open mouth of individual MNRJ 26928 showing the black throat lining. All depicted individuals are adults.

Anolis species in GenBank. Our sampling totaled 83 specimens from 66 *Dactyloa* species, as well as *Anolis bimaculatus* (Sparman, 1784), *Anolis cupreus* Hallowell, 1860, *A. fuscoauratus*, *Anolis lucius* Duméril and Bibron, 1837, *Anolis marcanoi* Williams, 1975a, *A. ortonii*, *Anolis smaragdinus* Barbour and Shreve, 1935, *Anolis tandai* Avila-Pires, 1995, and *Anolis trachyderma* Cope, 1876 as outgroups.

Sequences were edited and aligned using Geneious Pro 10 (<https://www.geneious.com>; Kearse et al., 2012). In the case of the RAG1 nuclear gene, we used Geneious' plugin Heterozygotes with a 0.90 overlap threshold to identify heterozygous positions. We selected models of nucleotide substitution using PartitionFinder 2.1.1 (Lanfear et al., 2016), implementing PhyML for likelihood estimation (Guindon et al., 2010) and the Bayesian information criterion for

model selection (Sullivan and Joyce, 2005). Due to the small size of individual tRNA genes (~70 bp), which might impair proper estimation of substitution parameters (Prates et al., 2015), these regions were treated as a single partition. We set branch lengths as "linked" and the list of models of nucleotide evolution as "beast", and compared partition schemes by gene (four partitions) or codons within each gene (10 partitions). Based on PartitionFinder results, codon partitions were implemented for the protein-coding genes ND2, COI, and RAG1 (i.e., three partitions per gene).

Inferring phylogenetic relationships and divergence times

We performed simultaneous phylogenetic inference and divergence time estimation for the *Dactyloa* clade of *Anolis*

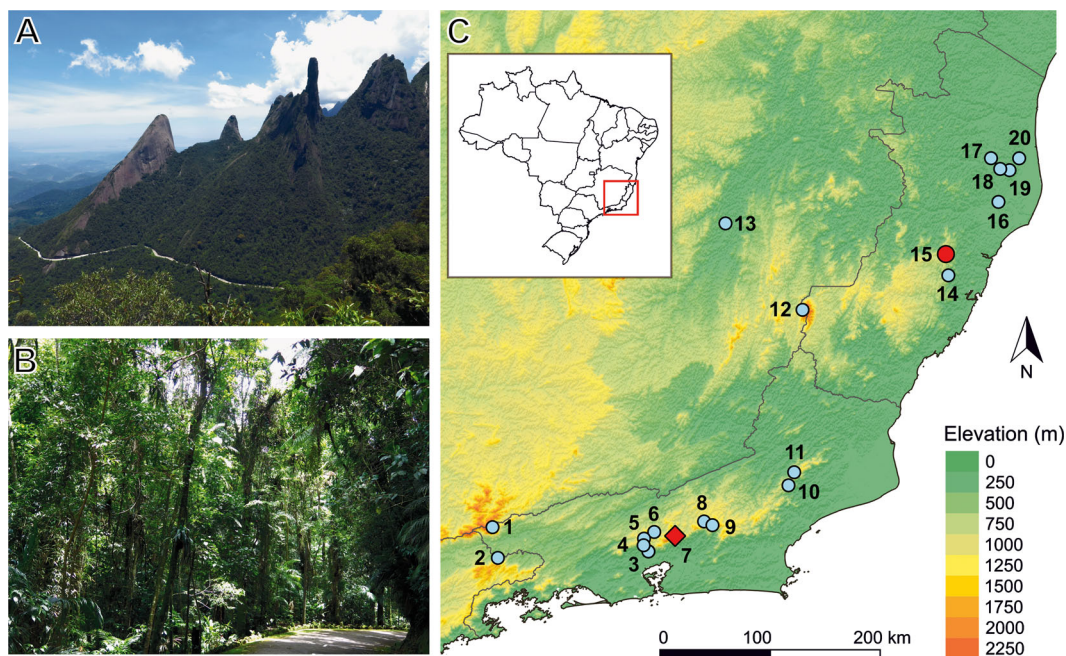


Figure 2. (A) Partial aerial view of the Serra dos Órgãos, type locality of *Anolis neglectus*, sp. nov. (B) Montane Atlantic Forest habitat where the new species was found. (C) Map depicting location of recent herpetological inventories (each lasting two to four weeks) in the states of Espírito Santo (ES), Minas Gerais (MG), Rio de Janeiro (RJ), and São Paulo (SP) in southeastern Brazil. Red diamond indicates the type locality of *Anolis neglectus*, sp. nov. Red circle indicates the site where *Anolis nasofrontalis* and *Anolis pseudotigrinus* are known to occur. Blue circles indicate sites where we failed to detect twig anole-like species. Sampled sites are: Parque Nacional de Itatiaia, RJ (1); Parque Nacional da Serra da Bocaina, SP (2); Duque de Caxias, RJ (3-4); Petrópolis, RJ (5-6); Parque Nacional da Serra dos Órgãos, RJ (7); Parque Estadual Três Picos, RJ (8-9); Parque Estadual do Desengano, RJ (10-11); Parque Nacional do Caparaó, MG (12); Parque Estadual do Rio Doce, MG (13); Santa Leopoldina, ES (14); Reserva Biológica Augusto Ruschi, ES (15); Floresta Nacional de Goytacazes, ES (16); Reserva Biológica Sooretama, ES (17); Reserva da Companhia Vale do Rio Doce, ES (18-20).

under a Bayesian framework using BEAST 1.8.4 (Drummond et al., 2012) through the CIPRES Science Gateway (Miller, Pfeiffer, Schwartz, 2010). We applied a birth-death process tree prior (Gernhard, 2008) and an uncorrelated log-normal relaxed clock (Drummond et al., 2006) for each locus separately. To improve the estimation of nucleotide substitution rates, we set a lower prior bound of 0.0001 to the corresponding rate parameters (Prates et al., 2017). No constraints of monophyly were enforced.

In the absence of *Dactyloa* anole fossils for time-calibration, we estimated divergence times following Prates et al. (2017). Briefly, we used published divergence times estimated based on nuclear genes and fossils calibrations (Prates et al., 2015) to assign a normally distributed calibration prior to two nodes: the most recent common ancestor (MRCA) of *Anolis phyllorhinus* Myers and Carvalho, 1945, *A. punctatus*, and *Anolis transversalis* Duméril in Duméril and Duméril, 1851 (mean = 17.5 millions of years ago; std. dev. = 3.5); and the MRCA of those three species and *Anolis dissimilis* Williams, 1965 (mean = 35.5; std. dev. = 5.5). To parameterize the mean rate of the molecular clock, we used rates estimated by Prates et al. (2016a) to assign a normally distributed prior to the mitochondrial locus ND2 and

flanking tRNAs (mean = 1.40×10^{-2} substitutions per site per million year; std. dev. = 5×10^{-3}) and the nuclear gene RAG1 (mean = 6.15×10^{-4} , std. dev. = 1.65×10^{-4}).

We performed three independent BEAST runs of 20 million generations each, sampling every 2,000 generations. We used Tracer 1.6 (Rambaut et al., 2018) to assess whether Markov chain mixing was adequate (effective sample sizes > 200) and to visually assess model parameter stationarity and convergence between runs. We then combined the three runs in LogCombiner 1.8.4 (with 10% of each run discarded as burn-in) and summarized a maximum clade credibility tree in TreeAnnotator 1.8.4 (Drummond et al., 2012). The resulting topologies were visualized in FigTree 1.4 (available from <http://tree.bio.ed.ac.uk/software/figtree>).

Gathering morphological data

Morphological measurements and scale characters follow Köhler (2014), except for the phalanx terminology, as we consider the concealed ungual phalanx as the first phalanx (following de Queiroz, Chu, Losos, 1998; ungual phalanx not considered in phalanx count by Köhler, 2014). Morphometric measurements were made on 15 preserved adult

specimens with a digital caliper to the nearest 0.1 mm. Sex was determined based on dewlap coloration, presence of hemipenes, and enlarged postcloacal scales in males. Color in life was obtained from field notes and photographs of recently collected specimens. To support biological inventories in the Atlantic Forest, we provide morphological comparisons with the other Atlantic Forest anoles based on the literature (Ávila-Pires, 1995; Prates et al., 2017) and analysis of specimens deposited in the Naturhistorisches Museum Wien (NHMW), Museu de Biologia Professor Mello Leitão (MBML), Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Coleção Herpetológica do Departamento de Zoologia da Universidade de São Paulo (MTR), Museu de Zoologia da Universidade de São Paulo (MZUSP), and Zoological Museum Hamburg (ZMH). See Appendix for a list of examined specimens and species.

Results

Phylogenetic relationships

Phylogenetic analyses (fig. 3) inferred five major clades within the *Dactyloa* clade of *Anolis* previously referred to as species series, namely the *aequatorialis*, *heterodermus*, *latifrons*, *punctatus*, and *roquet* series (Castañeda and de Queiroz, 2013; Poe et al., 2015, 2017; Prates et al., 2017). Nodal support for the relationships among major *Dactyloa* clades was generally low.

Anolis nasofrontalis, *A. pseudotigrinus*, and the new species formed a clade with six other species, five of which also occur in montane South American regions: *Anolis calimae* Ayala, Harris, Williams, 1983 from the Colombian Andes; *Anolis hyacinthogularis* Torres-Carvajal et al., 2018 and *Anolis lososi* Torres-Carvajal et al., 2018 from the Ecuadorian Andes; *Anolis williamsmittermeierorum* Poe and Yáñez-Miranda, 2007 from the Peruvian Andes; *Anolis neblininus* (Myers, Williams, McDiarmid, 1993) from the Neblina *tepui* mountain on the Brazil-Venezuela border; and *Anolis dissimilis* from southwestern Amazonia (fig. 3). This clade was inferred with weak support as sister to a clade composed of species previously assigned to the *roquet* species series (Castañeda and de Queiroz, 2013; Poe et al., 2017).

The new species from Serra dos Órgãos was inferred as the sister of *A. nasofrontalis*

with strong support. The MRCA of these two species is sister to *A. pseudotigrinus*, suggesting that the three montane Atlantic Forest anoles form a clade, although this relationship was weakly supported (fig. 3). These species were not closely related to *A. punctatus*, the fourth species of the *Dactyloa* clade known to occur in the Atlantic Forest.

Divergence time estimates indicate that the new species and *A. nasofrontalis* diverged in the early Pliocene, around 5.24 mya (HPD = 3.35–7.58 mya). The MRCA of these two species diverged from *A. pseudotigrinus* around 10.33 mya (HPD = 7.26–13.65 mya). The MRCA of these three Atlantic Forest species diverged from the western Amazonian *A. dissimilis* around 11.15 mya (HPD = 8.11–14.67 mya).

Within the *Dactyloa* clade, divergences between most sampled species predate the Quaternary, dating back to the Miocene (fig. 3). All major clades within *Dactyloa* started to diversify during the early Miocene and late Oligocene, mirroring the results of other recent studies (Prates et al., 2015, 2017).

Anolis neglectus, new species

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figs 1, 4–5

Holotype: MNRJ 26927 (field number LOD 1265), adult male (snout-vent length [SVL] 53.3 mm), collected in the Parque Nacional da Serra dos Órgãos (22°26'55.9"S, 42°59'09.9"W; 981 m above sea level), municipality of Teresópolis, state of Rio de Janeiro, Brazil, on 10 March 2015, by Leandro O. Drummond, Paulo R. Melo-Sampaio, and Renata M. Pirani.

Paratypes (n = 15): MNRJ 25116 (LOD 1264), adult male (SVL 55.3 mm); MNRJ 25117 (LOD 1266), adult female (SVL 56.7 mm); MNRJ 25118 (LOD 1269), adult female (SVL 61.5 mm); MNRJ 25119 (LOD 1270), adult female (SVL 59.3 mm); MNRJ 25120 (LOD 1271), adult male (SVL 54.9 mm); MNRJ 26930 (LOD 1258), adult male (SVL

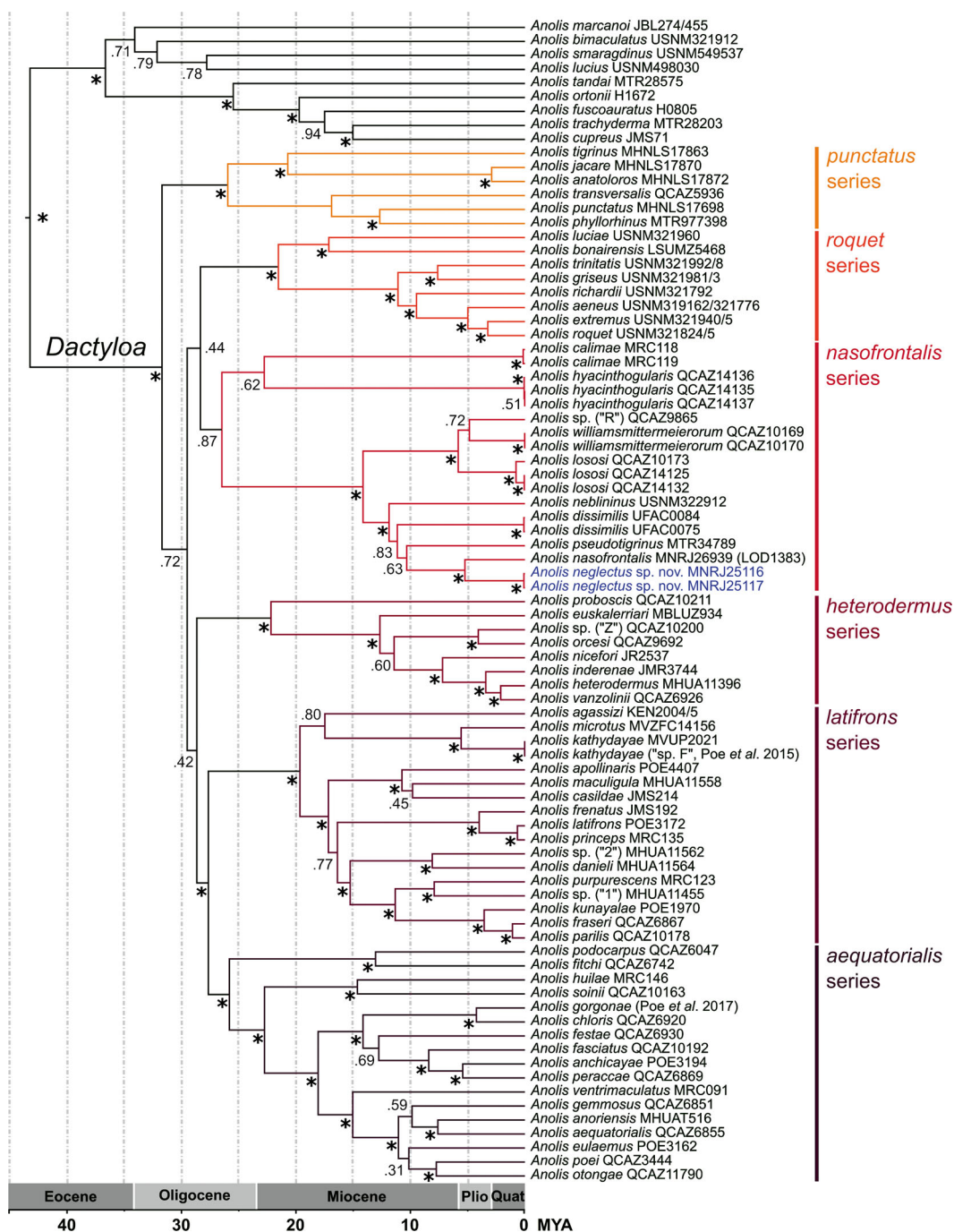


Figure 3. Phylogenetic relationships and divergence times for species in the *Dactyloa* clade of *Anolis*. Asterisks denote posterior probabilities > 0.95.

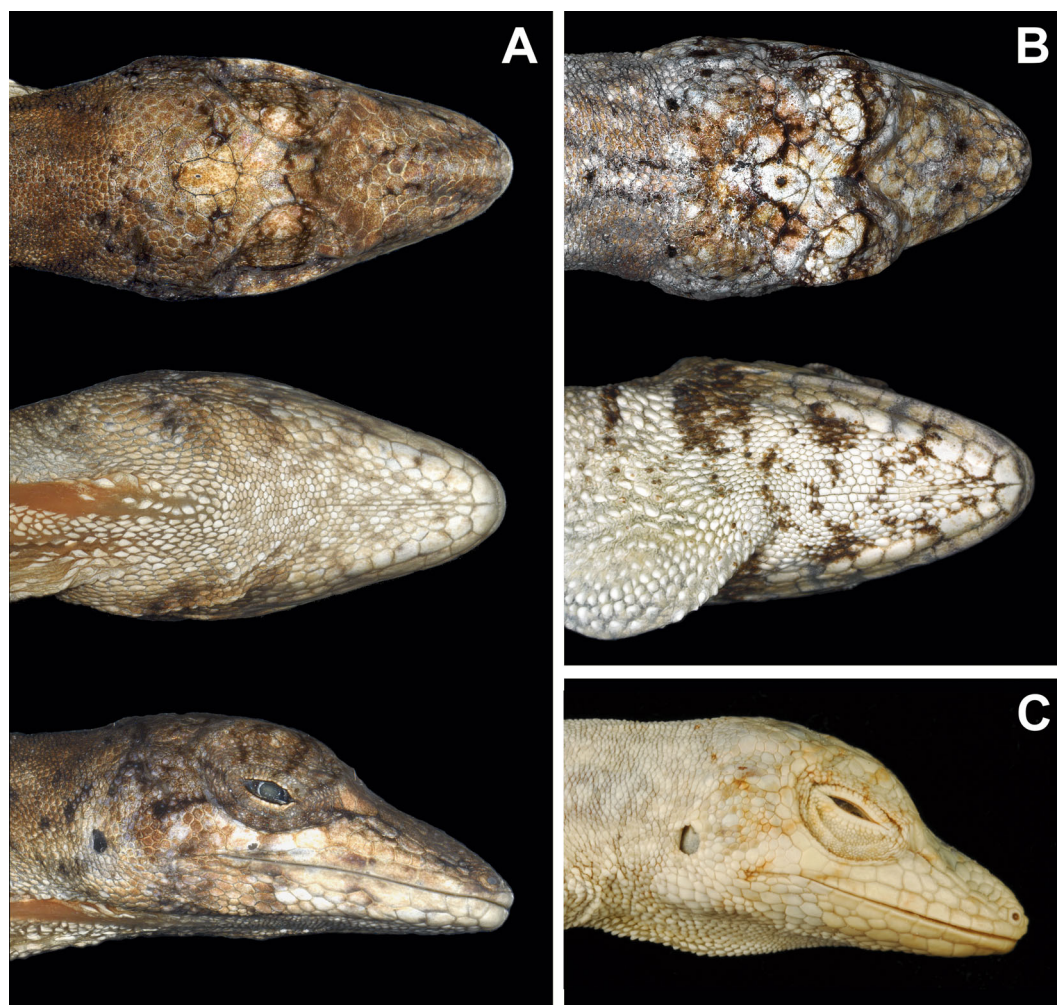


Figure 4. (A) Head of the holotype of *Anolis neglectus*, sp. nov. MNRJ 26927 in dorsal, ventral, and lateral views (SVL 53.3 mm). (B) Head of *Anolis nasofrontalis* MNRJ 26939 in dorsal and ventral views (SVL 52.8 mm). (C) Head of *A. nasofrontalis* NHMW 25201.1 in lateral view. All depicted individuals are adults.

51.4 mm); MNRJ 26931-32 (LOD 1259-60), adult females (SVL 62.7 mm and 60.7 mm, respectively); MNRJ 26933 (LOD 1261), juvenile female (SVL 29.4 mm); MNRJ 26934-35 (LOD 1262-63), adult females (SVL 58.5 mm and 60.4 mm, respectively); MNRJ 26936-37 (LOD 1267-68), adult females (SVL 62.2 mm and 55.1 mm, respectively); all specimens collected in the type locality between 8 and 10 March 2015. MNRJ 26928 (LOD 1139), adult female (SVL 54 mm); MNRJ 26929 (LOD 1140), adult male (SVL 53.8 mm); both collected in the type

locality on 16 February 2015, by Leandro O. Drummond and Paulo R. Melo-Sampaio.

Description of holotype (type series variation in parentheses): Snout-vent length 53.3 mm (51.4-54.9 mm in males, $n = 5$; 54.0-62.7 mm in females, $n = 10$); tail length 94 mm (77-94 mm in males; 89-104 mm in females); head length 13.2 mm (13.2-14.1 mm in males; 13.2-15.9 mm in females); head width 7.6 mm (7.2-8.1 mm in males; 7.3-8.5 mm in females); snout length 7.8 mm (7.8-8.1 mm in males; 7.5-8.8 mm in females); ear opening 0.4 mm (0.3-0.7 mm) horizontally, 0.7 mm

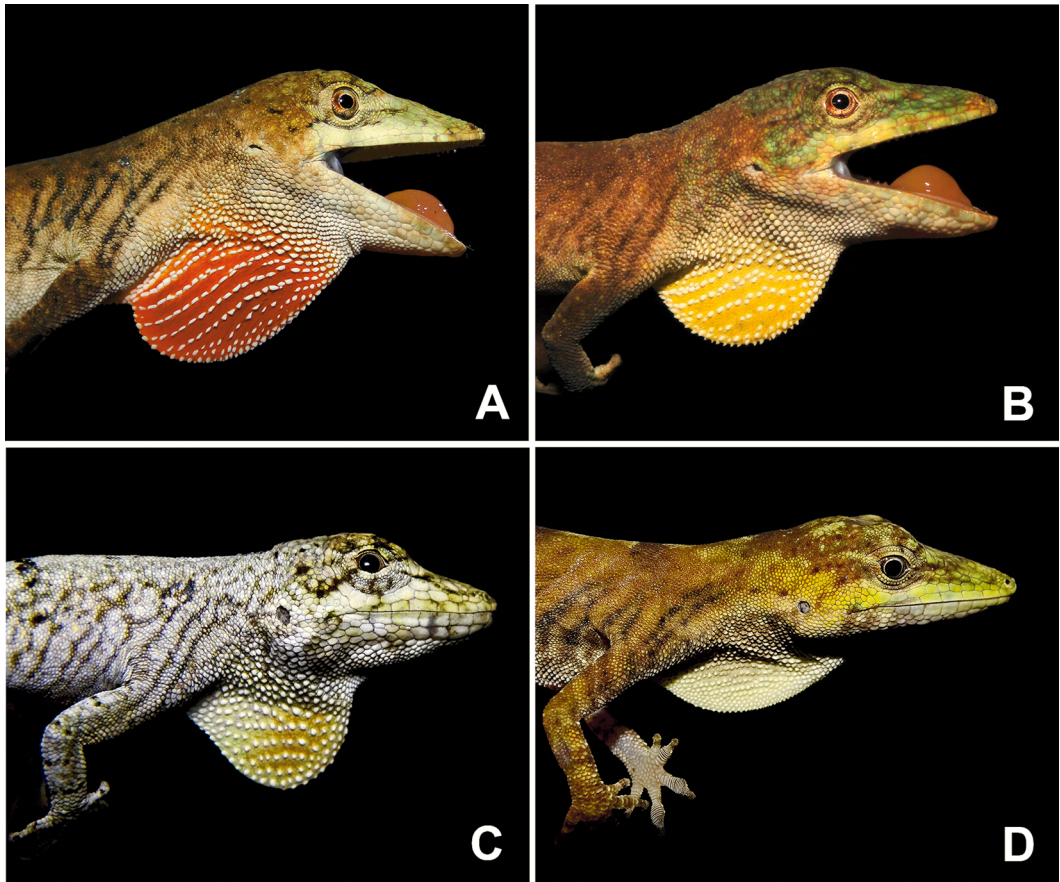


Figure 5. Dewlap patterns. (A) Adult male *Anolis neglectus*, sp. nov. MNRJ 25120, paratype. (B) Adult female *Anolis neglectus*, sp. nov. MNRJ 26932, paratype. (C) Adult female *Anolis nasofrontalis* MNRJ 26939. (D) Subadult female *Anolis pseudotigrinus* MNRJ 26938.

(0.7-1.2 mm) vertically; interparietal scale width 1.0 mm (1.0-1.6 mm), length 1.9 mm (1.4-2.1 mm); postcloacal scales wider than long and greatly enlarged, with width of 1.0 mm (1.0-1.6 mm); tail round in cross section; fourth toe of adpressed hind limb not reaching posterior insertion of arm; shank length 9.2 mm (9.1-9.6 mm in males; 9.1-10.4 mm in females); foot length 13.0 mm (11.2-13.9 mm); hand length 6.3 mm (6.3-7.4 mm); fourth finger of extended forelimb reaching about one third of the distance between eye and nostril (reaching about one third to half the distance); maximum width of subdigital pad of the forth toe 1.0 mm (1.0-1.3 mm); minimum width of subdigital pad of the forth toe 0.2 mm (0.2-0.3 mm).

Dorsal head scales smooth and juxtaposed (fig. 4); ventral head scales smooth and granular; prefrontal depression poorly defined; rostral slightly overlaps mental; six postrostrals (4-6); two prenasals (1-2), lower one in contact with rostral; circumnasal broadly in contact with rostral and first supralabial; four to six internasals; six supralabials to the level below center of eye (6-9); six infralabials to the level below center of eye on the right side, seven on the left side (5-10); four postmentals (3-6), the two external ones greatly enlarged; four enlarged sublabials in contact with infralabials on right side and five on left side (2-5); canthal ridge indistinct; 12 smooth loreals on right side and 11 on left side (9-19) disposed in three rows (2-3) at the

level of the second canthal; eight scales between first canthals (6-11); six scales between second canthals (5-9); three and four smooth suboculars (3-5) in broad contact with four supralabials (3-6); two slightly elongated to squarish smooth superciliaries above anterior portion of eye (1-3); two greatly enlarged smooth supraoculars (2-5); one complete row of circumorbitals separating supraoculars from supraorbital semicircles (row of circumorbitals absent to complete); supraorbital semicircles broadly in contact with each other (separated by one row of scales to broadly in contact) and in contact with interparietal plate (separated by one row of scales to broadly in contact); parietal depression shallow and ill-defined; interparietal distinctly enlarged, surrounded by large to moderate-sized scales; scales anterior and posterior to ear opening subequal, slightly larger anteriorly.

Dewlap moderate-sized (moderate in males and small in females) (fig. 5); anterior insertion of extended dewlap at the level of posterior border of eye; posterior insertion of extended dewlap at the level of posterior border of forearm (insertion at the level of the anterior border of forearm in females); about six rows of gorgetal-sternal dewlap scales (6-7 in males; 4-6 in females), as large as the ventral scales, separated by naked skin.

Dorsal body scales smooth and juxtaposed, mostly hexagonal; no enlarged rows of dorsals; 88 dorsals in a longitudinal row between the level of axilla and groin (86-101); lateral scales smooth, granular, rounded; ventrals smooth, imbricate, with rounded posterior margins, about twice the size of dorsals; 73 ventrals in a longitudinal row between the level of axilla and groin (64-73); 97 scales around mid-body (88-97); axillary depression or pocket absent; about 1/5 of proximal portion of tail with smooth, mostly hexagonal scales, remaining 4/5 bearing imbricate, mostly hexagonal scales, keeled in dorsal and strongly keeled in ventral region.

Supradigital scales smooth; 26 subdigital lamellae under proximal-middle phalanges of

fourth toe (24-31); six scales under the penultimate phalanx of fourth toe (5-7); penultimate phalanx raised above proximal ones; subdigital lamellae of toepad projecting distally under subdigital scales of the penultimate phalanx.

Color in life: Dorsal surface of body, head, tail and limbs with a lichenous pattern of dark-brown, dark-green or black lines, reticulations and dots on a light gray to light green background (figs 1, 4-5); in specimens stressed by handling, the background color tends to become darker with ferruginous and olive green shades (fig. 5A-B); about four pairs of diagonal lines on the flanks of the first half of body; irregularly distributed dark reticulations and/or amorphous spots on the second half of body; a dark and well-marked interorbital line present on dorsal surface of head; at least two other dark lines radiating from each eye, first one extending posteriorly halfway to tympanum, second one extending anteriorly along canthus rostralis, usually reaching the second canthal scale; iris light brown bordered by dark brown flecks; tail with six to ten faint to well-marked dark brown to black bands; ventral surface of head, body, tail and limbs light-gray with scattered dark brown spots; black throat lining (fig. 1E); tongue pink; female dewlap skin uniformly bright orange (fig. 5B); male dewlap uniformly dark red (fig. 5A); dewlap scales white.

Color in preservation: After being preserved in formalin and stored in ethanol, individuals acquired a gray to light brown background color. After four years of preservation, the dewlap skin of females lost their coloration and became cream, while that of males faded to reddish-orange (fig. 4).

*Species comparisons (data from species compared to *A. neglectus* in parentheses):* *Anolis neglectus* can be distinguished from the *Norops* clade Atlantic Forest species *A. fuscoauratus* and *A. ortonii* by 88-97 scales around mid-body (*A. fuscoauratus*: 124-157; *A. ortonii*: 123-180), smooth dorsals (weakly keeled), and smooth snout scales between nostrils (keeled). *Anolis neglectus* further differs from *A. fuscoauratus*

by a lichenous dorsal body coloration (brown or gray), supraorbital semicircles in contact (separated by granular scales) and well-developed dewlap in females (vestigial).

Three species of *Dactyloa* clade anoles are known to occur in the Atlantic Forest: *A. nasofrontalis*, *A. pseudotigrinus*, and *A. punctatus*. *Anolis neglectus* is distinguished from *A. punctatus* by its smaller size (in *A. punctatus*, maximum SVL of 90 mm in males and 81 mm in females), male maximum SVL smaller than that of females (larger), absence of protuberant snout in males (present), round canthus rostralis (angular), smooth or granular scales on body and head (keeled scales on dorsum, limbs, canthus rostralis, throat, chin and between rostrals), 88-97 scales around mid-body (132-167); moderate-sized red dewlap (when extended) in males with posterior insertion at the level of the posterior border of forelimbs (large white, yellow, or orange dewlap with or without scattered black spots and extending beyond the posterior border of the forelimbs), presence of dewlap in females (vestigial), and lichenous dorsal pattern (uniformly green).

The new species is similar to *A. pseudotigrinus* and *A. nasofrontalis* in morphology and coloration (fig. 5). It differs from *A. pseudotigrinus* by having a smaller size (in *A. pseudotigrinus*, 56.4-57.6 mm in males and 65.2-66 mm in females), hindlimb not reaching posterior insertion of forelimb when adpressed along the body (reaching), prefrontal depression shallow (deep); moderate-sized red dewlap (when extended) with posterior insertion at the level of posterior border of forearm in males (large dewlap with posterior insertion at about mid-belly; dewlap color of male *A. pseudotigrinus* unknown), four to seven rows of gorgetal-sternal dewlap scales (12-14), small and uniformly bright orange dewlap with insertion at the level of anterior border of forearm in females (large white dewlap with posterior insertion at the level of posterior border of forearm), presence of an interorbital dark line (absent), 64 to 73 ventrals in a longitudinal row between

the level of axilla and groin (79-90), 88-97 scales around mid-body (106-118), and absence of large dark blotches on the vertebral region of preserved specimens (present).

The new species is most similar to its sister *A. nasofrontalis*. It differs from *A. nasofrontalis* (figs 4-5) by having a longer and more pointed snout (shorter and more rounded) and prefrontal depression shallow (deep), female dewlap small with uniformly bright orange skin (dewlap orange yellow faded to white posteriorly), and male dewlap with moderate size (small) and uniformly dark red that turned reddish-orange in preservative (pink, faded to white posteriorly; Amaral, 1933). While the dewlaps of females of *A. neglectus* resemble those of females of *A. nasofrontalis*, we have not seen an orange yellow dewlap faded to white posteriorly (as seen in *A. nasofrontalis*) in any of the 18 females of *A. neglectus* that we have examined (see Appendix).

Recognition of the population from the Serra dos Órgãos as a distinct species is further supported by a >400 km geographic separation from closely related taxa and by its 5.24 mya estimated divergence from its sister *A. nasofrontalis*. This divergence is considerably deeper than those observed between several currently recognized species in the *Dactyloa* clade of *Anolis*. This is the case, for instance, for the divergences between: 1) *Anolis gorgonae* Barbour, 1905 and *Anolis chloris* Boulenger, 1898; 2) *Anolis parilis* Williams, 1975b, *Anolis fraseri* Günther, 1859 and *Anolis kunayalae* Hulebak et al., 2007; 3) *Anolis latifrons*, *Anolis princeps* Boulenger, 1902 and *Anolis frenatus* Cope, 1899; 4) *Anolis heterodermus*, *Anolis vanzolinii* (Williams et al., 1996) and *Anolis inderenae* (Rueda and Hernández-Camacho, 1988); 5) *A. roquet*, *Anolis extremus* Garman, 1987 and *Anolis aeneus* Gray, 1840; and 6) *Anolis jacare* Boulenger, 1903 and *Anolis anatorlos* Ugueto et al., 2007 (fig. 3).

Based on a more extensive sample of anole species (some represented only by morphological data), Poe et al. (2017) found *A. nasofrontalis* and *A. pseudotigrinus* to be closely

related to *Anolis laevis* (Cope, 1876), a species that was not included in our analyses due to the lack of genetic data. This species, which is known from a single site in the Andes of Peru, can be easily distinguished from *A. neglectus* by the presence of a rostral appendage (Williams, 1979).

Etymology: The specific epithet, *neglectus*, is a Latin name meaning “neglected” or “forgotten”. The name is a suitable reference to an arboreal lizard species that remained undetected despite over 200 years of zoological inventories in the Serra dos Órgãos, now a popular tourist destination close to the large city of Rio de Janeiro. The name also alludes to the tragedy that hit the Museu Nacional do Rio de Janeiro, Brazil’s first scientific institution, which became 200 years old in 2018. On September 2nd of that same year, after decades of negligence on the part of federal administrations, the Museum’s main building (the São Cristóvão Palace) was consumed by a catastrophic fire. The fire led to the destruction of public exhibits, laboratories, libraries, and up to 18 million items in the archaeological, anthropological, historical, and zoological collections. We propose “Serra dos Órgãos anoles” as the common English name of the new species, and “papa-ventos da Serra dos Órgãos” as the common name in Portuguese (in some places in Brazil, anole lizards are colloquially referred to as “papa-ventos”, “wind eaters”, because of their dewlaps).

Geographic distribution and natural history. We found all specimens of *A. neglectus* in an area smaller than one square kilometer in the Parque Nacional da Serra dos Órgãos in Teresópolis (fig. 2A). The area is characterized by secondary montane Atlantic Forest vegetation (fig. 2B). We spotted all but one out of 36 specimens (26 collected) during active searches at night along forest edge; a single individual (a juvenile female) was found active in a garden at approximately 4:00 pm. In one night, we spotted ten individuals between 9:00 pm and 1:00 am. At night, these lizards were found sleeping perched on the tips of twigs or other

narrow plant structures at a height of 1.5 to 8.0 m, with the ventral surface of the body and tail pressed against the substrate. Over a total of seven nights of search, we found a much larger number of females ($n = 28$; 18 collected) than males ($n = 8$). Males might be harder to detect due to their thinner bodies; moreover, it is possible that they perch higher on the vegetation, as no male was found less than 4 m above the ground. Observation of captured individuals during the day revealed that they move slowly and infrequently when placed on branches, keeping their body and tail in contact with the substrate. In two instances we placed two females on the same branch, after which they immediately started to perform displays by extending their dewlaps and lifting their tails.

Discussion

Systematics of Dactyloa clade anoles

Our phylogenetic results were largely consistent with previous studies of the *Dactyloa* clade within *Anolis* (Castañeda and de Queiroz, 2013; Poe et al., 2015, 2017; Prates et al., 2017). However, our analysis did not infer the same composition of species in the *heterodermus* series (sensu Poe et al., 2017). Instead, we found that a subset of the species previously assigned to the *heterodermus* series formed a clade that is sister to a clade composed of species previously assigned to the *roquet* series (Castañeda and de Queiroz, 2013; Poe et al., 2017), albeit with low support. That subset includes the Andean species *A. calimae*, *A. hyacinthogularis*, *A. lososi*, and *A. williamsmittermeierorum*; Guiana Shield *A. neblininus*; southwestern Amazonian *A. dissimilis*; and Atlantic Forest *A. nasofrontalis*, *A. pseudotigrinus*, and *A. neglectus* (fig. 3).

According to the definitions provided by previous studies (Castañeda and de Queiroz, 2013; Poe et al., 2017), the clade composed of those nine species would be considered part of the

roquet series within *Dactyloa*. However, similar to our study, previous investigations inferred weakly supported relationships between this clade (or subsets of it) and the other main *Dactyloa* subclades (Castañeda and de Queiroz, 2011, 2013; Prates et al., 2015, 2017; Poe et al., 2015, 2017). Because this clade is reasonably well supported and of similar age (and roughly similar species richness) to the five previously recognized main *Dactyloa* subclades, and because its relationships to those other clades remain uncertain, we propose to recognize this clade as its own series, as follows:

(*Anolis/Dactyloa*) *nasofrontalis* series, new clade name

Definition. The largest crown clade that includes *A. nasofrontalis* and excludes *A. aequatorialis* Werner, 1894, *A. latifrons* Berthold, 1846, *A. heterodermus* Duméril, 1851, *A. punctatus*, and *A. roquet* (Bonnaterre, 1789).

Reference phylogeny. Figure 3.

Composition. *A. nasofrontalis*, *A. neglectus*, *A. pseudotigrinus*, *A. dissimilis*, *A. neblininus*, *A. lososi*, *A. williamsmittermeierorum*, *Anolis* sp. “R” (Poe et al., 2015), *A. hyacinthogularis*, *A. calimae*, *A. carlostoddi* (Williams, Praderio, Gorzula, 1996), and *A. bellipeniculus* (Myers and Donnelly, 1996). Inclusion of *A. nasofrontalis* is necessitated by the definition. Inclusion of the next seven species is strongly supported by the results of our phylogenetic analysis. Inclusion of *A. hyacinthogularis* and *A. calimae* is weakly supported by those results. Inclusion of *A. carlostoddi* and *A. bellipeniculus*, for which DNA sequence data are currently lacking, is inferred from the results of other studies (e.g., Poe et al., 2017). Based on the results of Poe et al. (2017), it is possible that the poorly known *A. laevis* is also part of this clade.

Comments. This clade has previously been called the *neblininus* species series (Prates et al., 2017) based on the *neblininus* group of Williams, Praderio, Gorzula (1996). However, that name has so far been used only in the original publication, and we therefore here rename

it the *nasofrontalis* series based on the tradition in anole taxonomy of using the oldest name of a species in the group as the basis of the group’s name (Williams and Duellman, 1984; Savage and Guyer, 1989). The name “*neblininus* group” could be applied to a subclade of the *nasofrontalis* series including *A. neblininus* and its closest relatives (not including *A. nasofrontalis*).

The proposal of a sixth series clade within the *Dactyloa* clade of *Anolis* requires amending the phylogenetic definitions (de Queiroz and Gauthier, 1990, 1992) of the names of the other *Dactyloa* series. We here amend those definitions, using fig. 3 as a reference phylogeny, as follows:

***aequatorialis* series.** The largest crown clade that includes *Anolis aequatorialis* and excludes *Anolis heterodermus*, *Anolis latifrons*, *A. nasofrontalis*, *A. punctatus*, and *Anolis roquet*.

***heterodermus* series.** The largest crown clade that includes *A. heterodermus* and excludes *A. aequatorialis*, *A. latifrons*, *A. nasofrontalis*, *A. punctatus*, and *A. roquet*.

***latifrons* series.** The largest crown clade includes *A. latifrons* and excludes *A. aequatorialis*, *A. heterodermus*, *A. nasofrontalis*, *A. punctatus*, and *A. roquet*.

***punctatus* series.** The largest crown clade that includes *A. punctatus* and excludes *A. aequatorialis*, *A. heterodermus*, *A. latifrons*, *A. nasofrontalis*, and *A. roquet*.

***roquet* series.** The largest crown clade that includes *A. roquet* and excludes *A. aequatorialis*, *A. heterodermus*, *A. nasofrontalis*, *A. latifrons*, and *A. punctatus*.

Because this and previous investigations have consistently inferred low support for the phylogenetic relationships between major *Dactyloa* clades (Castañeda and de Queiroz, 2011, 2013; Prates et al., 2015, 2017; Poe et al., 2017), we refrain from comparing the deeper relationships inferred by us and other studies. Resolving these relationships will likely entail more comprehensive sampling of genetic variation in these lizards.

Biogeography of montane Atlantic Forest anoles

Mountains in the southern Atlantic Forest region harbor a high diversity of narrowly distributed species. Among the mechanisms proposed to explain this pattern is the idea that what are currently montane habitats have persisted in the face of climatic fluctuations over time, perhaps through down and upslope movement, favoring species accumulation (Amaro et al., 2012; Carnaval et al., 2014). This hypothesis is supported by genetic investigations of vertebrate taxa, which have found signatures of population persistence on southern Atlantic Forest mountains over tens to hundreds of thousand years (Thomé et al., 2010; Amaro et al., 2012; Carnaval et al., 2014; Firkowski et al., 2016). Long-term population persistence in mountains also seems to characterize the history of *A. neglectus* and its relatives *A. nasofrontalis* and *A. pseudotigrinus*. To test population stability through time in these secretive lizards, future studies will rely on an improved sampling of individuals and genetic variation to perform historical demographic inference.

Our molecular analyses inferred a deep divergence between *A. neglectus* and its sister *A. nasofrontalis*, dating back to 5.24 mya. Isolation-by-distance (IBD) seems insufficient to explain the observed genetic divergence between these two species. IBD would predict ongoing or recent genetic exchange across the 400 km-long transect that separates known populations of *A. nasofrontalis* and *A. neglectus*. However, the available evidence strongly supports that these species are not continuously distributed. This portion of the Atlantic Forest is Brazil's most studied and best-known region from a biological standpoint (Moura et al., 2018). Our own work has failed to detect anoles similar to these two species during herpetological inventories (each lasting from two to four weeks) in 18 sites (fig. 2) located around and between Santa Teresa (where *A. nasofrontalis* occurs) and Serra dos Órgãos (where *A. neglectus* was

found). While undetected populations are a possibility in these cryptic lizards, a scenario of genetic continuity across the landscape, with differences resulting from IBD, seems unlikely.

Disjunct distributions between *A. neglectus* and *A. nasofrontalis* may be explained by the existence of a cold-adapted ancestor that occurred in the intervening lowlands in the past, a scenario invoked to explain similar biogeographic patterns in anurans (Firkowski et al., 2016). A scenario of downhill movement and dispersal, or of fragmentation of a previously continuous distribution, may also explain close phylogenetic relationships between endemic anoles that occur in the southern Atlantic Forest, Andes, and Guiana highlands, mountains separated by hundreds to thousands of kilometers (Prates et al., 2017). Our analysis of divergence times in the *Dactyloa* clade suggests that these distributional changes took place in the Miocene and early Pliocene.

While the available evidence supports that these montane anoles are absent from lowland Atlantic Forest, several other mountains occur between the Serra dos Órgãos (state of Rio de Janeiro), where we collected *A. neglectus*, and Santa Teresa (state of Espírito Santo), where *A. nasofrontalis* and *A. pseudotigrinus* occur. Among them are highlands in the Parque Estadual do Desengano and the Parque Estadual Três Picos, where we performed two 15-day-long biological inventories in late 2016 (fig. 2). However, we did not detect *Anolis* lizards. Future herpetological inventories in the mountains of the states of Rio de Janeiro, Espírito Santo, and Minas Gerais should be attentive to arboreal lizards with small size, short limbs, and cryptic coloration, characteristics shared by *A. neglectus*, *A. nasofrontalis*, and *A. pseudotigrinus*.

Due to its body proportions and coloration, *A. neglectus* is reminiscent of members of the Caribbean twig anole ecomorph. A twig anole morphology occurs in several other montane South American *Anolis* species (Williams, Praderio and Gorzula, 1996; Losos et al., 2012; Poe et al., 2015; Prates et al., 2017), several of

which are members of the *heterodermus* series. This pattern, which may be indicative of convergent evolution, deserves closer examination under a comparative ecomorphological framework.

Conservation remarks

Anolis neglectus is known only from the Parque Nacional da Serra dos Órgãos, a protected area of 10 653 ha within an Atlantic Forest fragment in the state of Rio de Janeiro. While occurring in a national park, this montane species may be at risk due to human-driven climatic change. By leading to upslope shifts in species ranges, rising temperatures reduce available habitat for montane species (Colwell et al., 2008; Sinervo et al., 2010). Moreover, lower temperatures and higher rainfall on mountains increase the deposition of persistent airborne pollutants (Daly and Wania, 2005). At Serra dos Órgãos, Meire et al. (2012) recorded legacy and current-use pesticides, with *chlorpyrifos*, *endosulfan*, and *hexachlorocyclohexane* being the most abundant contaminants. Attesting to the prevalence of these contaminations, we serendipitously discovered *A. neglectus* while performing a toxicological survey that recorded increased deposition of atmospheric mercury with elevation (Drummond, 2017).

In the survey that discovered *A. neglectus*, we also sampled reptiles and amphibians at 34 sites between 325 and 2181 meters above sea level in the Parque Nacional da Serra dos Órgãos. However, we found all individuals of the new species at a single site close to the park's visitor center, near the boundary between the park and the city of Teresópolis. It is currently unclear how the intense flow of tourists (around 100 000 visitors per year) and the presence of free-roaming dogs and cats may affect this lizard species. New surveys in additional sites will be crucial to gather density, distribution, and natural history information, shedding light on the conservation status of this neglected anole species.

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Appendix

Specimens examined

Anolis nasofrontalis (n = 8): Holotype MZUSP 440, adult female from Espírito Santo (ES), Brazil; allotype MZUSP 440.A, subadult male from ES, Brazil; ZMH R0411, adult female from Santa Leopoldina, ES, Brazil; NHMW 12742, NHMW 25201.1, and NHMW 25201.2, adult females from Santa Leopoldina, ES, Brazil; MNRJ 1625, adult female from Santa Teresa, ES, Brazil; MNRJ 26939 (field number LOD 1383), adult female from Reserva Biológica Augusto Ruschi, Santa Teresa, ES, Brazil.

Anolis pseudotigrinus (n = 9): Holotype MZUSP 721.B, adult female from “Rio Doce region”, ES, Brazil; MZUSP 36718, adult male from Santa Teresa, ES, Brazil; MBML 327, adult female, MBML 266 and 536, two adult males, and MBML 554, subadult male, from the park of the Museu de Biologia Professor Melo Leitão in Santa Teresa, ES, Brazil; MTR 34789 and 34790, two adult females from the Reserva Biológica Augusto Ruschi, ES, Brazil; LOD 1237, subadult female from Reserva Biológica Augusto Ruschi, ES, Brazil.

Anolis neglectus sp. nov. (n = 26): Holotype MNRJ 26927, adult male; paratypes MNRJ 25116, MNRJ 25120, MNRJ 26929-30, all four adult males; paratypes MNRJ 25117-19, MNRJ 26928, MNRJ 26931-32, MNRJ 26934-35, MNRJ 26936-37, all 10 adult females; paratype MNRJ 26933, juvenile female; MNRJ 27093 (field number PRMS 469), 27094 (PRMS 471), 27095 (PRMS 475), PRMS 472-73, MTR 41752-53, all seven adult females; PRMS 470, subadult male; PRMS 474, MTR 41751, two adult males; all specimens from Parque Nacional da Serra dos Órgãos, Teresópolis, RJ, Brazil.